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PLANT SUCCESSION IN THE NORTHEASTERN PORTION OF THE PEACE-ATHABASCA DELTA, ALBERTA

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Plant succession in the northeastern portion of the Peace-Athabasca Delta, Alberta" submitted by Michael Joseph Patrick Doherty in partial fulfillment of the requirements for the degree of Master of Science.

ABSTRACT

This study, conducted during the growing seasons of 1970, 1971, and part of 1972, involved examinations of the environment and vegetation of 165 zones at 16 sites in five ecologically distinct areas in the northeastern portion of the Peace-Athabasca Delta, Alberta. The vascular flora of the study region is characterized by 59 families, 160 genera, and 292 species. This study has increased the knowledge about the floral composition of the delta by the addition of 21 new species.

Sixteen community types were recognized by the author, using the minimum variance technique of cluster analysis of Pritchard and Anderson. Six subtypes were also recognized. Three additional community types on Precambrian Outcrops were investigated subjectively.

Each community type occupied a relatively distinct position in the deltaic landscape. Topographic, physiographic, and hydrologic regimes influenced the flora and vegetation. Additional factors in the edaphic regime were also important.

Soil development, environment stability and amelioration, age, and biotic structure, interaction, and organization generally increased with succession. Species

diversity and understory biomass showed variable trends. Average herb-dwarf shrub, shrub, and tree covers generally increased with succession but remaining vegetation attributes exhibited less distinct trends.

Hydric succession to the Upland Forest Community Type in the study region takes about 170 years which is much greater than the time mentioned by Dirschl for a comparable vegetation type to develop. The "climatic climax" species in the study region is *Picea glauca* while "edaphic climax" species in the Bog and Precambrian Outcrop Community Types are *P. mariana* and *Pinus banksiana*, respectively.

Prominent species, vegetation units, and pathways differed from those presented by Raup and Dirschl *et al.* for the delta.

Annual flooding has clearly prevented the Marsh Community Type from undergoing gradual succession to the Upland Forest Type. In the delta, flooding and not burning as suggested by some investigators for other parts of Alberta is the dominant factor retarding succession.

The flora and vegetation are closely adjusted to natural fluctuations in the hydrologic regime. Any natural or artificial stabilization of hydrologic conditions will drastically alter the dynamic nature of the vegetation on flood prone areas. Thus, stabilization will accent ombrotrophic and oligotrophic conditions and

promote abnormally rapid senescence of the delta. Any attempt to prevent stabilization of the hydrologic regime will further minerotrophic and eutrophic conditions and prolong the life-time of the Peace-Athabasca Delta.

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INTRODUCTION

Of the world's inland-freshwater deltas, the Peace-Athabasca (PA) is not only one of the largest, at over 3800 km^2, but also the most extensive one located wholly within the boreal zone. This delta may be characterized as a flat, lacustrine-alluvial plain that is liberally endowed with flowing and standing water bodies. The only relief is provided by scattered, granitic outcrops and knolls, and by levees and terraces occurring along distributaries. The constant meandering of these distributaries in the floodplain has resulted in erosion of upstream areas producing cut-back levees and in build-up of downstream areas such as slip-off slopes. The meandering process has also contributed greatly to typically very complex site, vegetation, moisture, and drainage patterns.

The delta possesses extensive wetland vegetation types which provide suitable habitats for one of the continent's largest herds of bison, for large populations of moose and muskrat, and for numerous bird species, especially waterfowl. Land use in the delta has, so far, been limited to selective logging for white spruce, fur

trapping, hunting, fishing, and conservation. However, the completion in 1968 of the W. A. C. Bennett hydro-electric dam on the upper Peace River in British Columbia may have had an indirect influence on the delta which may affect these activities. Similarly, construction of oil sands extraction complexes near Fort McMurray, Alberta, may affect the delta via the Athabasca River (Fig. 1).

The PA delta is composed of coalescent deltas of the Athabasca, Peace, and Birch Rivers at the western end of Lake Athabasca in northeastern Alberta. The study region for this thesis consists of back-water basins and levee areas along the Rivière des Rochers and its fork, the Revillon Coupé, which are situated in the northeastern portion of the delta. Five ecologically distinct study areas (Revillon Coupé, Lake Athabasca Marsh, Chilaway Snye, Egg Lake, and Nuphar Lake) comprise the study region (Fig. 1).

The Revillon Coupé (RC) study area has an inundational area of *ca.* 4 km^2 through which the Coupé River meanders after leaving the Rivière des Rochers some 18 km NW of Fort Chipewyan and joining, further north, the Peace River about 14 km upstream from the Peace-Rochers-Slave junction (Fig. 1). The channel is relatively straight for considerable stretches, varies in width from 25-90 m and has an average relief of 4-9 m with 1970-72 mean summer water levels (MSWL's) approximately midway between the

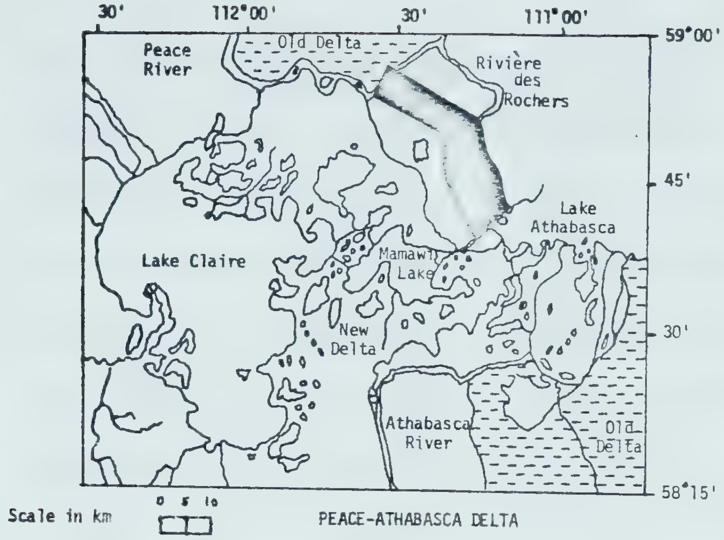


Figure 1. Location maps of the five study areas, including 16 sites, in the northern portion of the Peace-Athabasca Delta, Alberta.

channel bottom and levee top. Because of its direct connection to the Peace and Rochers, lower riparian and levee areas are exposed to all floods, but only during high flood periods occurring at spring break-up are higher areas liable to be inundated. During spring break-up, erosion of cut-banks in upper sections of the study area is enhanced by higher flow rates, ice and wave actions, and water levels. During post-flood periods, water levels frequently fluctuate 10-25 cm in a day, and reverse direction in response to flow differentials in main channels and to changes in Lake Athabasca water levels. With late summer stabilization of flow direction and water levels, erosive processes almost cease, revealing recently deposited alluvial sediments especially in lower sections of the study area. Previous erosion-sedimentation cycles have created a distinct channel-and-levee topography which, when not influenced by granitic outcrops, generally consists of a series of narrowly to broadly parallel benches joined by steep to shallow walls to form an irregularly spaced step-like pattern of alluvial terraces which are either paired or unpaired. Vegetation cover generally increases with each successive bench-step, but terraces located below MSWL are mostly devoid of vegetation. A typical zonal sequence of *Equisetum* spp. —> *Salix* spp. —> *Alnus tenuifolia* —> *Populus balsamifera* —> *Picea glauca* is highly correlated with increasing height and age of each terrace, and each zone forms a compressed

but quite distinct, discontinuous stage (Pl. 1). In older portions of the area, ridge-and-swale topography is very pronounced with ridges dominated by *P. glauca* and swales by subhygrophytic species. Soils show a progressive development corresponding closely with plant successional stages. They are generally coarse to very coarse textured with Orthic Regosols predominating.

The Lake Athabasca Marsh (LAM) study area consists of extensive, medium-textured alluvial flatlands situated along the anastomosing network of outflow channels from Lake Athabasca. These flatlands extend some 10 km NNW of Fort Chipewyan (Fig. 1). Because of its direct contact with the Rivière des Rochers and the outflow channels, this study area receives sediment from the Peace during flood periods early in the growing season and is irrigated by east wind-tides when the lake is ice-free. Sedimentation rather than erosion is the predominant process in the study area. Elevations of sampled LAM zones were 50-100 cm above mean summer water level (ASWL) in 1970, so this study area is annually inundated for much if not all of the growing season, *e.g.* in 1971 and 1972. Study sites were dominated by both open and closed graminoid vegetation, typically *Phragmites communis*, in 1970-72. Scrub cover, dominated by *Salix* spp., mostly occurred on slightly higher levee crests bordering the channels (Pl. 2). The vegetation

Plate 1. Typical vegetation pattern in the Revillon Coupé study area showing site #3. Note the parallel arrangement and stratification of the vegetation.

Plate 2. Typical vegetation pattern in the Lake Athabasca Marsh study area showing site #3. Note the location and development of clones of *Phragmites communis*.

exhibits a horizontally extended zonation. Soils are essentially inorganic, interstratified sediments having relatively high silt and clay contents. The wetland soils are exclusively Gleyed Regosols.

The Chilaway Snye (CS) study area consists of a shallow, depositional basin with an inundational area of *ca*. 2 km^2 located at the end of what is now a closed, reversing-flow channel, 5 km long, leading to the Rivière des Rochers at a point 4 km south of the Rochers-Coupé junction (Fig. 1). Because this channel is considerably deeper than most of the CS basin, it can flood and drain the latter rapidly and efficiently. Most of this gently undulating basin is covered by very fine-textured interbedded sediments. This area was covered by sedge at an elevation of 10-100 cm ASWL during 1970 and 1971 even though flooded in early summer and for brief periods during and after east windstorms on Lake Athabasca. Flood waters usually remain in meadow areas behind levee crests for only a small part of the growing season. Although channel water levels did not fluctuate much on a daily basis, the range of fluctuations over the 1971 growing season was 250 cm. The CS area is controlled essentially by processes of sedimentation rather than erosion. The broad meadow zones were dominated by graminoid vegetation, typically *Carex atherodes*, while the upland periphery was bordered by large, old *Salix* clumps in a rather narrow

but distinct zone (Pl. 3). The lowland soils are predominantly Rego Gleysols.

The Egg Lake (EL) study area is a shallow and essentially flat (except for the occasional rock outcrop) back-water lake basin with an inundational area of *ca.* 15 km^2. The study area is located 6 km SE of the Peace River and, in a few places, is only 50 m from the Revillon Coupé (Fig. 1). Well-developed levees have progressively isolated the basin from the Peace and Coupé such that extensive flooding only occurs about once in every ten years. These floods take place when heavy runs of ice collect and jam in narrow stretches of the Peace River (*e.g.*, between points A and B in Fig. 1), and the build-up of water, ice, and sediment behind the ice dam breaches the levee and pours into Egg Lake. Since this water body has a perched water table resulting from the deposition of medium- to fine-textured sediments, flood waters once admitted are retained by levees at a new and higher level, and fluctuate very little except upward after heavy precipitation or rapid snowmelt. During the years following flooding, there is a gradual net drawdown in the water level since evapo-transpiration exceeds precipitation. There is also a long-term accumulation of organic matter. Lowland zones were dominated by several relatively productive aquatic, wet meadow, and meadow vegetation types during 1970-71. These types exhibited

Plate 3. Typical vegetation pattern in the Chilaway Snye study area adjacent to site #1. Note the areal extent of channel vegetation appreciably affected by annual flooding and drawdown.

distinct and horizontal zonal patterns that are strongly correlated with water depth because the water table is stable and near the surface for most of the year. The vegetation consists predominantly of graminoids, with some scrub and sparse tree cover (Pl. 4). The wetland soils are exclusively Orthic Gleysols.

The Nuphar Lake (NL) study area is a shallow, back-water lake basin occurring in an isolated drainage system with an area of less than 2 km^2 which has not been flooded for many years. The area is located NE of Egg Lake behind the levee on the opposite bank of the Coupé, and is surrounded on three sides by Precambrian outcrops (Fig. 1). The water table lies at or just below the bog surface throughout the year. Water levels fluctuated very little during the summers of 1970-72. Nuphar Lake sites were dominated by relatively stable and unproductive bog communities that are well correlated with water depth. These sites have consolidated moss carpets supporting some shrubs and a few trees which, together, take part in the typical successional sequence leading to *Picea mariana* bog woodland (Pl. 5). The vegetation zonation was horizontally compressed and quite distinct. The presence of ice in organic soils beneath *Sphagnum* hummocks is a major factor affecting soil and vegetation dynamics in the area.

Plate 4. Typical vegetation pattern in the Egg Lake study area near site #2. Note the scattered dead clumps, and dense and parallel arrangement of *Salix* spp.

Plate 5. Typical vegetation pattern in the Nuphar Lake study area at the NW end of the lake. Note the abundance of *Nuphar variegatum* and the more extensive development of tree species at the edge of the bog mat.

OBJECTIVES

This study was undertaken in the northeastern portion of the Peace-Athabasca delta with the following objectives in mind:

1. to describe the wide spectrum of botanical variation in the delta

2. to classify and describe the deltaic vegetation units

3. to analyze and describe the environments of the deltaic vegetation units

4. to characterize the deltaic flora and vegetation in relation to major environmental factors, mainly the hydrologic regime

5. to describe the important successional relations of the deltaic vegetation

6. to compare the findings in this study with those made by other investigators in the Peace-Athabasca Delta

7. to assess the effects on the deltaic flora and vegetation of any imposed stabilization of the regional hydrology.

METHODS

I SELECTION OF STUDY AREAS, SITES, AND ZONES

Potential study areas were located using advice from Drs. W. A. Fuller and G. H. La Roi, and Mr. Horace Wylie, topographic maps (1:250,000), aerial photographs, and ground observations. Each area was then examined and accepted if it differed from others in relation to the following criteria:

1. the type of connection to major distributaries
2. the depth and duration of spring and summer flood waters
3. the amount and rate of water-level fluctuation during the growing season (May to September)
4. the uniqueness of the vegetation.

Based on combinations of these criteria, five ecologically distinct study areas were selected.

Within each study area, potential "study sites", *i.e.* areas having specific widths and variable lengths extending from open water to inland locations or the far side of islands, and possessing numerous vegetation zones, were accepted if the following conditions were satisfied:

1. adequate geographical spacing
2. distinct vegetation sequence typical for the study area
3. minimal topographic variation, *e.g.* in the number of ridges and swales

4. approximately the same effects from flooding
5. minimal anthropogenic, pyric, and faunal disturbance
6. suitable accessibility.

Using these criteria, 16 study sites were selected.

At each site, potential "zones", *i.e.* concentric or parallel areas having relatively uniform physical and, if present, vegetational characteristics, were examined and accepted for subsequent analyses if the following criteria were met:

1. a relatively uniform environment
2. a relatively unform physiognomy
3. an area equalling or exceeding the smallest appropriate sampling unit
4. distinct species assemblages.

Using these criteria, 165 zones were chosen.

Of the 16 study sites selected (see Fig. 1, p. 3), five were chosen for intensive investigation as follows:

1. site #3 in the RC study area
2. site #1 in the LAM study area
3. site #1 in the CS study area
4. site #2 in the EL study area
5. site #1 in the NL study area

II TOPOGRAPHY

When all the criteria had been fulfilled, the topographic variation for all sites was assessed by levelling with a Brunton compass along a bearing normal to the vegetation zonation. The profile was started in the water and finished on the far side of islands, at high-levee, or upland locations.

III FLORISTICS

Representative voucher specimens are deposited in the University of Alberta Herbarium (ALTA). Nomenclature for vascular plants followed that used in "Flora of Alberta" by Moss (1959). Vegetative specimens of *Salix* spp. were keyed out according to Raup (1959). In each zone, a species abundance list was compiled for all species, including those not present in quadrats of the vegetation analysis.

IV VEGETATION ANALYSIS

A. Sampling Procedure

The stratified random procedure involved laying out a baseline along the same compass bearing used to assess the topographic variation and projecting, from the mid-point of each zone, a second baseline perpendicular to the first. This second line ran almost parallel to zonal boundaries for a maximum of 50 m. The centre of each nested quadrat was located using two random numbers; the first determined the distance along the second baseline, and the second delimited the perpendicular distance from the second baseline to the quadrat centre. Quadrats were alternately positioned on either side of the second baseline such that they did not overlap or come within 5 m

of the first baseline. This procedure was followed in most cases; however, certain modifications were made to compensate for changing zonal dimensions and to reduce edge-effects from adjoining zones. In these instances, the left side of the first baseline was utilized.

The number of quadrats necessary to account for variations in species abundance was determined by constructing species-area graphs for some zones in major vegetation types. Five quadrats were sufficient to analyze the flora in each stratum because all high-cover species had been recorded and most other species had been noted.

Quadrat sizes were 1 m x 1 m, 2 m x 2 m, and 5 m x 5 m; larger-sized quadrats would have been too large for narrow zones and smaller-sized quadrats would have greatly increased the field time required to achieve the same sampling intensity and precision.

B. Vegetation Cover

Actual species cover was estimated as the ground area occupied by the vertical projection on to it of the aerial parts of the individuals. This cover was recorded as a percentage of the total quadrat area to the nearest 5%. Mean species cover values were calculated for each zone and converted to cover classes, mid-points of which were used in subsequent analyses (App. 1). The cover of species

rooted outside the sampled zone was not taken, except for cover estimates of each stratum.

For sampling terrestrial vegetation, a centrally nested quadrat system was utilized; a 1 m x 1 m quadrat was enclosed by a 2 m x 2 m which, in turn, was enclosed by a 5 m x 5 m quadrat. For sampling aquatic vegetation, a 1 m x 1 m quadrat frame was constructed using four lengths of wood lashed together to form the appropriate area. At two corners of the frame, wire loops were attached so that poles could stabilize the frame in one location while sampling was being conducted from a canoe.

C. Analysis of Vegetation Attributes

A 1 m x 1 m quadrat was used in the herb-dwarf shrub stratum to record the cover of herbs and, also, dwarf shrubs which were less than 30 cm in height. In addition, dwarf shrub density was estimated.

A 2 m x 2 m quadrat was used in the shrub stratum to record the cover of shrubs and, also, tree transgressives that were greater than 30 cm in height and less than 3 cm in diameter at breast height (dbh). In addition, average heights and densities of both live and dead individuals were evaluated.

A 5 m x 5 m quadrat was used in the tree stratum to record saplings with 3-8 cm dbh and, also, trees with stems greater than 8 cm dbh. Average heights, densities,

and dbh's of both live and dead individuals were noted. For all tree species, the basal area for live and dead individuals was tallied using the Bitterlich 10x prism from centres of nested quadrats. Tree cover was assessed using a Lemon spherical densiometer.

Subjective estimates of vitality were made for each species in every quadrat using modified Braun-Blanquet scales (App. 1). For all quadrats, total percentage covers for lichens, mosses, and liverworts, and for herb-dwarf shrub, shrub, and tree strata were taken when present.

In each zone, species dispersion was noted using a modified Braun-Blanquet scale (App. 1).

D. Biomass Sampling

Terrestrial samples were harvested from herb-dwarf shrub and shrub strata in each zone of intensive study sites during the last week of June and the first week of July 1971. A nested quadrat was located at the mid-point of each zone and on the left side adjacent to the first baseline. All live (chlorophyll portion) moss and above-ground herbaceous vegetation was clipped while all the current year's growth was collected for woody species. Samples were weighed and air-dried in the field. These samples were later oven-dried in the laboratory at 80°C for 24 hours, and weights recorded and converted to kg/ha.

These converted weights have been presented in the following growth-form groups: bryoids, graminoids, forbs, dwarf shrubs, and shrubs. The aquatic vegetation was harvested and weight determined using the method outlined by Van Der Valk (1970:23), and expressed as kg/ha of dry matter.

E. Community Age Determination

Depending on community physiognomy, 3-5 increment cores were taken at breast height for each tree species and 3-5 disc samples were taken at ground level for each shrub species. Height and dbh were recorded for each tree, and height for each shrub sampled. Various size classes were included in the samples in order to determine community age structure, possible date of community establishment, and successional status of species and community. Average community age was obtained using the mean for the oldest woody species in the primary tree, sapling, or shrub canopy. In the case of communities with only a herb-dwarf shrub stratum, an approximate age was attained through seedling ring-counts or through the predominance of perennials, biennials, or annuals.

F. Moisture Status Classification

The subjective designation of hydrophytic, subhydrophytic, hygrophytic, subhygrophytic, mesophytic, submesophytic, subxerophytic, and xerophytic moisture

classes to flora and vegetation was based on soil moisture properties, soil aeration (evidence of gleying and mottling), surface and soil drainage, soil texture and organic matter, and flood-water, water-table, and water-body levels in each zone.

V ENVIRONMENTAL ANALYSIS

A. General Description

For all quadrats, the total cover of detritus, "woody detritus" (naturally fallen or flood-deposited woody stems and branches), bare soil, and water was taken. In addition water depth, microrelief, physiographic position, and pyric damage were recorded when appropriate. Soil drainage class based on criteria presented by Lacate (1965:6) and Canada Department of Agriculture (1970:215) was also recorded.

B. Edaphic Variables

i. Soil Profile Description

A soil pit was dug at a central representative location of each zone in the five intensive study sites during the 1971 growing season. A detailed profile description was made in which each horizon was characterized. Presence of free lime in each horizon was determined using a 10% HCl solution. Evidence of flooding expressed as gleying, mottling, oxidation-reduction

laminae and beds, buried organic layers, and interstratified laminae and beds of sands, silts, and clays was noted. Soil profile variability was assessed when texture and moisture samples were obtained at later dates. Soil nomenclature follows that used in "The Canadian System of Soil Classification" by Canada Department of Agriculture (1978).

Samples for later mechanical and chemical analyses were taken from each horizon, air-dried, and stored. These samples were sieved to obtain a <2 mm humus and mineral fraction. The samples were sent to the Alberta Soil and Feed Testing Laboratory to obtain semi-quantitative information about organic matter, sulphate, sodium, and free lime, and quantitative data concerning pH, conductivity (mmhos/cm) for soluble salts, and available nitrogen as nitrate, phosphorus, and potassium in kg/ha (converted from lb/acre). To facilitate comparison among soil attributes having semi-quantitative data, the following digital conversion scale was used, where L = Low, M = Medium, and H = High: insignificant (0.5), L^- (2), L(3), L^+ (4), M^- (5), M (6), M^+ (7), H^- (8), H (9), and H^+ (10).

ii. Soil Texture and Moisture Properties

Samples were taken from four corings within a 5 m radius of the mid-point of each zone during the latter half of the 1971 growing season. Except for soil pits, textural samples were taken at the 15-30 cm interval of

each zone. For all samples, the percentage sand, silt, and clay fractions were determined by the revised hydrometer method (Bouyoucos 1951).

Soil moisture samples, subsampled from the 15-30 cm interval, were weighed in the field and later oven-dried at 105°C in the laboratory. Water content was expressed as a percentage of the oven-dried weight of the soil. All samples taken from this interval were used to determine the available soil water expressed as the difference between field capacity (determined by using a porous, ceramic-plate, pressure-extraction apparatus at 1/3 bars) and permanent wilting percentage (using a similar apparatus at 15 bars).

C. Hydrologic Regime

i. Water Levels

A water-level gauge was established at each intensive site and the relative water-level fluctuation determined, based on the initial reading. Gauge readings were recorded on a daily (RC, EL) or weekly (LAM, CS, NL) basis.

ii. General Observations

Notes on water-table level, water temperature, water flow direction, substrate stability, wave action, flooding depth and duration, ice scouring effects, and

species and vegetation responses were made, when appropriate, throughout the growing season in all study areas.

VI SUCCESSIONAL STATUS

All zones in the study region were rated as to successional status (*e.g.*, pioneer, transitional, or terminal stage) according to the degree of control exerted by allogenic (environmental factors acting from outside the vegetation unit), autogenic (biotic processes acting within the vegetation unit), or polygenic (mixture of environmental factors and biotic processes acting upon the vegetation unit) factors. The criteria affecting the above determinations, as modified from Gill (1971), are:

1. for allogenic factors

   a. presence of mor formation in a poorly developed soil profile which generally lacks an Ah horizon
   b. absence of distinct buried organic layers in the soil profile, probably reflecting annual flooding which prevents surface accumulation of appreciable organic matter
   c. presence of interstratified sediment layers having different textural contents
   d. presence of oxidation-reduction bands
   e. presence of the current year's sediment deposition covering, either partially or totally, the previous year's litter
   f. absence of a well-developed moss layer
   g. presence of flood tolerant species (A few species adaptations to flooding are the presence of large air spaces between cells, the ability of root cells to tolerate the accumulation of ethanol under anaerobic conditions, and the production of adventitious roots.)

2. for autogenic factors

   a. presence of mull formation in a well-developed soil profile which generally has a distinct Ah horizon
   b. absence of buried organic layers, probably reflecting the relatively high rate of litter decomposition
   c. absence of interstratified sediment layers
   d. absence of oxidation-reduction bands
   e. absence of sediment deposition on the previous year's litter which is in varying degrees of decomposition
   f. presence of an abundant moss layer
   g. presence of flood intolerant species

3. for polygenic factors

   a. presence of distinct buried organic layers in the soil profile, probably reflecting relatively long flooding periods and indicating soil depositional history
   b. various combinations of the above criteria for both allogenic and autogenic factors

VII VEGETATION CLASSIFICATION

Cluster analysis is a polythetic, agglomerative, hierarchical technique (Pritchard & Anderson 1971). The analysis was performed using the following five variations: nearest neighbour, furthest neighbour, group average, centroid clustering, and minimum variance (main programme written by P. W. Conway, University of Alberta, and subroutines supplied by A. J. B. Anderson, Medical Research Council, Edinburgh, Scotland). It was used to obtain community type groupings.

VIII NOMENCLATURE

Nomenclature of each plant community is based on a species having the highest prominence value (PV = % mean cover x $\sqrt{\%\ \text{frequency}}$) in tree, shrub, and herb-dwarf shrub strata. This stratal sequence is maintained throughout the thesis. Each stratum is separated by a slash mark. Nomenclature of each community type is similarly based, except the tree and shrub strata may be dropped if their characteristic species have relatively low PV's and an occurrence of less than 60%. Under this system of nomenclature a woody species can possibly characterize the herb-dwarf shrub stratum and other strata, *e.g.* in the *Alnus tenuifolia/A. tenuifolia* community.

DELTAIC ENVIRONMENT

I CLIMATE

The regional climate of the PA delta is characterized by cool, short summers and cold, long winters of the subarctic zone (Dfc) of the Köppen classification in Trewartha (1954). Observations made during the 1941-1970 period at Fort Chipewyan indicate that adjusted mean daily, and mean daily maximum and minimum temperatures are *ca.* -3^{o}, 3^{o}, and $-9^{o}C$ respectively. The mean daily temperature in July, the warmest month, is *ca.* $16^{o}C$ and in January, the coldest month, it is *ca.* $-26^{o}C$ (Environment Canada: Atmospheric Environment 1975). Lake Athabasca and other water bodies may have some moderating influence as the delta exhibits lower summer and higher winter temperatures, and frost-free periods about 20 days longer than those in the surrounding uplands (Raup 1935, Longley 1968). The frost-free period usually extends from early June to mid-September (Dirschl *et al.* 1974).

Mean annual precipitation at Fort Chipewyan during a 10-year period is *ca.* 320 mm of which *ca.* 211 mm falls during the growing season (Peace-Athabasca Delta Project

Group [PADPG] 1973). The mean annual lake evaporation is *ca.* 406 mm, which slightly exceeds precipitation (PADPG 1973).

The prevailing wind direction during the growing season is from the northwest (Odynsky 1958).

During periods of diminished mountain runoff and deltaic precipitation, water levels in distributaries and in back-water basins continue to recede until minimum levels are reached in late winter. At this time the delta usually begins to recharge with the following year's spring and summer upper watershed runoff. Absence of flooding in conjunction with high temperatures, reduced precipitation, and increased evaporation will enhance the drawdown effect. During these drawdown periods certain changes in wind direction and velocity are important in irrigating and maintaining some wetlands of the delta. For example, preliminary studies conducted by the PADPG (1973) indicate that an easterly wind having a velocity of 21 km/hr sustained for 6 hrs or more will produce a 0.3 m seiche effect on Lake Athabasca and in areas adjoining the lake such as LAM and CS. Additional effects are produced in flow direction in the Revillon Coupé depending upon water-level relationships within the hydrologic network. Thus, climatic factors of temperature, precipitation, evaporation, and wind have an important bearing on water levels, especially when there is a shortage in water

supply from rivers entering or adjacent to the delta (PADPG 1973).

II GEOLOGY

The study region is situated in a post-glacial interphase between the Laurentian Plateau Province to the east and the Mackenzie Lowland Province to the west and north (Camsell & Malcolm 1921). This interphase generally follows closely the eastern border (*i.e.*, along the Rivière des Rochers and Athabasca River) of Wood Buffalo National Park almost to its southern boundary (Raup 1946).

Precambrian rocks associated with the Laurentian Plateau underlie the study region at a maximum depth of 61 m (Bayrock & Root 1972). These rocks are composed of Archean granites and gneisses, and to a lesser extent of undifferentiated rocks consisting of more ancient metamorphosed sediments and basic intrusives (Raup 1930, 1946). They exhibit rugged and variable bedrock relief, occupying approximately 15% of the landscape as outcrops in the northeastern part of the study region and as isolated knolls in the southeastern periphery and areas southwest of Fort Chipewyan.

Surficial deposits of sand, silt, and clay overlie the bedrock of the study region and contribute considerably to the geologic complexity of the whole delta. On the

basis of texture and genesis, Bayrock (1962) classified sand deposits into the following categories: outwash, lacustrine, deltaic, alluvial, and aeolian. These sand deposits occur predominantly in the old delta (first delta formed by the Peace and Athabasca Rivers), while silt and clay sediments make up the major portion of recent alluvial deposits of the study region and present delta (see Fig. 1, p. 3). Recent alluvial sands containing pockets of gravel and silt are also found but are limited in extent.

Comprehensive descriptions of the geology of the PA delta and adjacent areas are given by the preceding authors as well as by the following investigators: Camsell (1917), McLearn (1917, 1918), Alcock (1936), Blake (1956), Carrigy (1959), Fahrig (1961), and Govett (1961).

III GEOMORPHOLOGY

In the Paleozoic Era epicontinental seas deposited sediments which covered some western areas of the Laurentian Plateau forming a disconformity. These areas were later modified by a regional uplift and subsequent erosion before Mesozoic seas invaded and laid down deposits. These deposits were then removed exposing Devonian beds which were later covered by fluvial sediments. The southwest advance of the Keewatin Ice Sheet completed the erosive process by

totally removing all sediments and remaining beds as well as some shield rocks from the study region and surrounding area (Tyrrell & Dowling 1896).

During the process of discontinuous glacial retreat which ended about 10,000 B.P. when the ice sheet left northeastern Alberta (Stelck 1967), four proglacial lake stages were formed. As the ice retreated, uneven isostatic re-adjustments occurred. These "rebounds" increased the tilting of the Lake Athabasca basin, producing drainage patterns and land-water relations similar to those at present (Alcock 1920, Bayrock & Root 1972). During the last stage, western and southern portions of the basin began to act as a settling area for both in- and out-wash sediments, forming a delta (termed the old delta) of the Peace and Athabasca Rivers. Today, this delta is characterized by a broad, level plain that has levees, meandering streams, and ponded cut-off channels (Raup 1930). This delta is generally composed of coarse sands overlaid, in places, by fine to medium alluvial sands which were subjected to intensive aeolian action to form dunes (Bayrock 1961, 1962, Lacate 1965).

As the water level in Lake Athabasca dropped, a new delta (the present Peace-Athabasca) was formed in reponse to a lower base-level. As a result, this delta is being built up by slower-flowing waters containing more silts and clays than sands. The two deltas have contributed to the low, broad, and level appearance of the

Mackenzie Lowland Province (Camsell & Malcolm 1921, Bayrock 1962).

The new delta exhibits a typical bird's foot pattern displayed as successive active lobe migrations producing over-lapping lobes with interbedded sediments (Bayrock & Root 1972). During a series of unusually high flood periods levees along major river courses are breached, initiating the formation of a new series of levees and distributaries. These channels commonly bifurcate and reunite to form an anastomosing network enclosing depressions that eventually become shallow lakes and wetlands. As these channels build out into Lake Athabasca the distributaries become overextended. At this time, deposition ceases and abandonment of the system begins. During this process the major river course shifts into an adjacent but minor distributary which has a steeper gradient to the lake basin. The deserted lobe is then inundated by lake waters as sediment compaction and subsidence takes place. According to Bayrock and Root (1972), the Athabasca River may eventually flow through or around the delta without depositing sediments into the area. A similar development has taken place for the Peace River and its delta as the river normally bypasses its own delta flowing directly into the Slave River. Thus, the inland delta is a geologically short-term phenomenon (Bayrock & Root 1972).

IV HYDROLOGY

A. General

At present, the PA delta is an intricate interconnecting hydrologic system in which Lake Athabasca is the focal point. Although most deltaic distributaries and lakes are involved in this system, only those of the Lakes Claire-Mamawi network, channels of the Peace and Athabasca Rivers, and distributaries of the Chenal des Quatre Fourches, Rivière des Rochers, and Revillon Coupé are important in controlling hydrologic patterns in the delta (see Fig. 1, p. 3). Relative differences in water levels in the Peace River and Lake Athabasca determine flow direction, flow rate, and average water levels of the deltaic water bodies. The higher Lake Athabasca is in relation to water levels in the Peace River, the greater the outflow will be into the Slave River via Rivière des Rochers, Chenal des Quatre Fourches, and Revillon Coupé. However, a southward flow into Lake Athabasca occurs via Lakes Claire-Mamawi network and other members of the system, if Peace River water levels are high. When water levels in the Peace River and Lake Athabasca are equal, the system is effectively dammed on the Slave River so that there is neither in- or out-flow. Thus, the Peace River has an important effect upon water levels in the delta, sometimes preventing flood waters of the Athabasca River

from proceeding down the Slave River. Variations in slope and natural obstructions such as ice- and log-jams and beaver and hydrologic dams add to the complexity of water movements and vegetation patterns in the system. Various deltaic hydrologic accounts have been given by Collier (1960), Coulson and Clark (1962), Coulson and Adamcyk (1969), Coulson (1970), Schultz (1970), Bennett (1970, 1971), Bailey (1971), Kellerhals (1971), and PADPG (1973).

B. Water-level Fluctuations

Relationships between water-level fluctuations and aquatic and terrestrial vegetation have been recorded by Buell and Buell (1941), Brown (1943), De Gruchy (1952), Johnsgard (1956), Robel (1962), and Stockton and Fritts (1973). The extent to which water-level fluctuations influence certain vegetation patterns in the study region has been previously discussed by Doherty and La Roi (1973).

Water-level fluctuations in the RC and LAM study areas are significantly different at the 5% probability level (using unpaired t-test) from those of the EL and NL areas. This difference is clearly reflected in species compositions of the four areas. The latter two study areas may be generally referred to as isolated drainage types that are usually associated with inactive portions of the delta. In the case of the perched EL basin, inundation occurs during over-levee flooding while the NL

basin is almost never flooded. Water-level fluctuations in these lake basins also result from surface runoff, precipitation, evapo-transpiration, and seepage loss. The CS study area is considered a restricted drainage type associated with active and semi-active portions of the delta. Water levels in the Snye fluctuate on a small scale even though connected by a channel to the Rivière des Rochers. The same replenishment and removal factors operate in this basin as in the isolated drainage type except that inundation is more important. The RC and LAM study areas may be referred to as open drainage types that have fluvial and riparian areas associated with active portions of the delta. Water-level fluctuations in distributaries of the RC and LAM study areas are closely associated. Factors determining in- and out-flow in this drainage type are identical to those observed in the above cases except that inundation and subsequent drawdown are most important.

During naturally occurring low water-level periods, such as in 1944-46 and 1968-71, which appear to happen on a recurring basis, the abundance and vitality of terrestrial plant species increases (Fuller 1951, Bennett 1971). During the 1968-71 period, terrestrial species were invading the increasingly more mesic zones adjacent to declining water levels. This invasion, although taking place in all study areas during 1970, was most noticeable in the

EL study area in 1971 when higher water levels covered the previously exposed zones in the RC, LAM, and CS study areas. The 1972 flooding of all areas, except NL whose vegetation showed no appreciable change during field studies, halted the drying trend in the study region and re-established wet conditions similar to those existing prior to the 1968-71 period. These wet conditions markedly reduced the abundance and vitality of mesophytic species, and favoured hydrophytic species in flood-susceptible areas. Thus, any significant change in the natural hydrologic regime initiates corresponding adjustments within the vegetation which has concomitantly developed and adapted to particular ranges in water-level fluctuations.

C. Ice and Snow

Some effects of ice action on vegetation have been previously described by Croxton (1939), Günzl (1953), and Gill (1971). In a study conducted by Doherty and La Roi (1973), it was found that ice action in and along the Revillon Coupé channel is an important mechanical factor in shaping physical habitats and structures of susceptible plant communities. Generally the affected vegetation zones displayed a simplified structure, reduced abundance and vitality of their major species, and often a large decrease in species richness. In other study areas the

presence of ice and snow was usually more important than the mechanical action of moving ice in determining distribution patterns of plant species and vegetation zones. However, it was found that ice-scouring does occur at rare intervals in the EL basin. Except for NL, other study areas may also be rarely or frequently affected by severe ice action, which produces devastating ecological effects on the vegetation.

D. Water Chemistry

Effects of water chemistry on the aquatic and semi-aquatic vegetation of the study region have been reported previously by Doherty and La Roi (1973). We found that by using pH and chloride values, the five water bodies may be classified into two groups. The "soft water group" is represented by NL, and the "hard water group" by remaining study areas. Except for differences in pH and chloride concentrations, chemical compositions of the five water bodies do not seem different enough to have an important selective influence on the nature and distribution of their vegetation. Thus, it appears that non-chemical factors are more important in controlling differential species occurrences among the water bodies. More detailed studies are required, however, before the effects of water chemistry on the aquatic vegetation can be completely assessed because of the

general and limited data, and the wide variations of other environmental factors present not only among areas but also within each area.

E. Sedimentation and Erosion

Effects of sedimentation on the vegetation in riparian and deltaic regions have been discussed by Ellis (1936), Harper (1938), Featherly (1941), Dahlskog (1966), and Edwards (1969). In a study conducted by Doherty and La Roi (1973), it was found that each study area may be characterized by suspended (turbidity) loads in its summer waters. We observed that the quantity and quality of sediments contained in flood waters is an important factor in the survival and distribution of certain species on the delta. In addition, variations in type and extent of the zonation among and within study areas are partly an expression of the organic/inorganic nature of the suspended load, and amount and rate at which the load is carried and deposited. For example in the RC study area, riparian species are aligned according to their tolerance ranges to changing inorganic loads and sedimentation rates.

Erosion is the dominant process occurring in upstream sections of the Revillon Coupé with sedimentation being more important in downstream sections. Erosion is effected by flooding, ice abrasion and scouring, wave action, and undercutting and slumping processes. In all

other study areas except for NL, the dominant process is sedimentation. The EL basin is, on rare occasions, scoured heavily by ice, while the NL basin is little eroded because of adequate levee separation from flood-water channels. In the former basin the dominant geomorphological process is still mineral sedimentation, while in the latter the build-up of the lake bed is achieved through deposition of plant organic matter. In these basins the shorelines are protected by vegetation, and the lakes are either of insufficient size or depth to permit wave erosion. However, water movements do permit redistribution and sorting of the deposited sediments and organic matter in them.

V TOPOGRAPHY

In the RC study area, the topography is quite complex and variable. In the youngest and lowest levee crests near the Rochers, slight topographic variations of up to 1.5 m ASWL exist. These levees are generally poorly to imperfectly drained and have mostly hygric and subhygric herbs and shrubs. At the other end of the channel, in the oldest and highest levee crests near the Peace River, the relief increases to 9 m ASWL. These older levees are usually well-drained and have mesophytic forests dominated by *Picea glauca*. Between these two

sections, intermediate levee heights, drainage and moisture conditions, and physiognomic types are observed. The vegetation along the Coupé is quite distinct and discontinuous responding to flooding and its effects, and to sharp topographic breaks such as slopes in cut-banks and terraces steps. Backslope locations of the area have hydrophytic to mesophytic vegetation types occurring in sloughs, oxbow lakes, flood scour routes, abandoned channels, point bars, and ridge and swales. These poorly to imperfectly drained locations exhibit a complex topographic variation that ranges up to about 4 m.

In the LAM and CS study areas, the topography is very subdued, with a relief up to 1 m ASWL. The hygrophytic to submesophytic vegetation types, mainly marsh, meadow, and fen, exhibit indistinct and continuous mosaic patterns in poorly to imperfectly drained lowlands.

Back-water areas of the study region (*e.g.*, EL and NL) also have slight topographic variations of up to 1 m ASWL. Microrelief in these areas is increased by the formation of sedge and peatmoss hummocks. The vegetation types (hygric to subhygric bog in NL, and subhygric meadow and fen in EL) occur in lowlands which are very poorly to imperfectly drained.

Areas lying above any maximum flood levels, such as Precambrian outcrops, have a relief varying up to about 50 m and a distinct but poorly developed subxerophytic and

xerophytic vegetation. These granitic areas are rapidly drained and occur, in varying extent, in all study areas.

VI SOILS

A. Introduction

In the Mackenzie Lowlands Section of the Boreal Forest Region, Halliday (1937) reported that Podzols were the predominant soil type while Rowe (1959, 1972) reported Gray Luvisols and Eutric Brunisols on well-drained sites, Regosols on alluvium, and Organic soils in the remainder of the lowlands. Lindsay *et al.* (1962), during an exploratory soil survey of the PA delta region, recognized Regosols, Gleysols, Gray Luvisols, Brunisols, Podzols, and Organic soils. Except for Brunisols, similar Great Soil Groups were found in the study region, but the soils were further classified to the Subgroup level. Results of soil textural analyses from samples taken from the 15-30 cm solum interval within each zone are given in Appendix 2. Results of soil chemical analyses from samples taken from the 0-90 cm interval of selected zones at certain sites are given in Appendix 3. The soils of intensive study sites for each study area are described below and subsequently related to flooding, drainage, vegetation, and physiographic position along a "catena" (topographic gradient).

B. The Revillon Coupé Study Area

This area has parent materials consisting of recent water-sorted alluvium. The texture of the soils is predominantly sandy loam with pH values neutral (7.0-7.2) and alkaline (7.4-7.8; App. 4).

The Levee Catena

Soils of this catena are stone free, and show either relatively constant or increasing pH values with profile depth. Soil development is related to improving drainage conditions, increasing height above MSWL's, and decreasing flooding effects. Mottling generally increases downward throughout each profile. This catena is under the influence of allogenic, polygenic, and autogenic factors.

1. The Low-levee Section

Orthic Regosol was situated in a well-drained and very gently sloping location at site #3, zone #19, under a *Salix lutea-S. interior/Equisetum arvense* community.

Horizon	Thickness	Description Date - 21 June 71
Ck	0 - 90 cm	Brown (10YR 5/3 d) and interstratified beds of pale brown (10YR 6/3 d) sandy loam$_1$ (S 50; Si 44; C 6) and of yellowish brown (10YR 5/4 d) sandy loam$_2$ (S 68; Si 26; C 6) having strong brown (7.5YR 5/8 d) to brownish yellow (10YR 6/6 d) mottles (25-40%) throughout; amorphous to single grain; firm to loose (m); strongly to weakly cemented; few roots and pores; abrupt to clear and smooth boundaries; pH 7.7 to 8.1.

This was the least developed soil type in the catena. Influence of annual flooding was strongly exhibited in the profile by the absence of litter and presence of mottling throughout the numerous interstratified sand beds, and in the vegetation by sparse herb and shrub strata composed of flood-adapted species. The presence of the same textural class throughout the soil profile suggested that flooding and its effects have been relatively uniform during the "development" of this soil type. This zone is controlled entirely by allogenic factors.

2. The Mid-levee Section

Orthic Regosol was situated in a well-drained and very gently sloping location at site #3, zone #27, under an *Alnus tenuifolia/A. tenuifolia* community.

Horizon	Thickness	Description Date - 5 July 71
L	trace	Grayish brown (10YR 5/2 d) deciduous leaf litter; pH 7.0.
Ck	0 - 90 cm	Brown (10YR 5/3 d) with yellow (10YR 7/6 d) mottles (1-5%) occurring in the upper 50 cm; sandy loam (S 61; Si 31; C 8); single grain; loose (m) to very friable; weakly cemented; few roots and pores; pH 7.2.

This soil type is more developed than that of section 1. The presence of sparse litter cover and much less profile mottling suggests that this zone has been less frequently flooded, and then only briefly with relatively more clay deposited than in the previous profile. The species

composition and a better developed herb and shrub strata also indicate that annual flooding is not as influential here. A higher topographic position, reducing some effects from annual flooding, is a major influence controlling profile development in this section. This zone is also controlled entirely by allogenic factors.

3. The High-levee Section

Cumulic Regosol was situated in a moderately well-drained and gently sloping location at site #3, zone #30, under a *Populus balsamifera/Cornus stolonifera/Rosa acicularis* community.

Horizon	Thickness	Description Date - 5 July 71
LFH	2 - 0 cm	Dark grayish brown (10YR 4/2 d) to grayish brown (10YR 5/2 d) semi-decomposed deciduous leaf litter; pH 6.8.
Ck	0 - 7 cm	Brown (10YR 5/3 d); sandy loam (S 57; Si 33; C 10); very fine single grain; loose (m); weakly cemented; plentiful roots and pores; clear and smooth boundary; pH 7.1.
Ahb	7 - 8 cm	Dark grayish brown (10YR 4/2 d) organic matter; pH 7.4.
Ck_1	8 - 12 cm	Yellowish brown (10YR 5/4 d); sandy loam (S 57; Si 33; C 10); fine single grain; loose (m); weakly cemented; few roots and pores; clear and smooth boundary; pH 7.0.
Ahb_1	12 - 14 cm	See Ahb
Ck_2	14 - 35 cm	Yellowish brown (10YR 5/4 d) to brown (10YR 5/3 d); loam (S 50; Si 35; C 15); very fine single grain; loose (m); weakly cemented; few roots and pores;

Ck_2 (cont'd)		clear and smooth boundary; pH 7.0.
Ahb_2	35 - 36 cm	See Ahb
Ck_3	> 36 cm	Yellowish brown (10YR 5/4 d) to brown (10YR 5/3 d) with reddish yellow (7.5YR 6/6 d) mottles (50%) occurring *ca.* 61 cm; sandy loam (S 59; Si 31; C 10); very fine single grain; loose (m); weakly cemented; very few roots amd pores; pH 7.4.

This soil type is more developed than the preceding one because of an LFH layer. Buried organic layers indicate previous flooding periods of considerable but infrequent duration during which greater relative amounts of silt and clay were deposited in this profile than in the two preceding types. The degree of influence exerted by flooding, exhibited as mottling resulting from fluctuating water-table levels, is not as strong as in the preceding soil type. A higher topographic position, insuring protection from most floods, is a major factor permitting profile development in this section. This situation is reflected in the species composition and well-developed strata. This zone is controlled by polygenic factors.

4. The Upland Section

Orthic Gray Luvisol was situated in a well-drained, and gently undulating location at site #3, zone #33, under a *Picea glauca/Rosa acicularis/Cornus canadensis* community.

Horizon	Thickness	Description Date - 5 July 71
LFH	1 - 0 cm	Very dark grayish brown (10YR 3/2 d) semi-decomposed coniferous and deciduous litter; pH 5.8.
Ah	0 - 5 cm	Dark brown (10YR 3/3 d); sandy loam (S 60; Si 27; C 13); single grain; loose (m); weakly cemented; plentiful roots; common pores; gradual and smooth boundary; pH 7.4.
Aej	5 - 31 cm	Brown (10YR 5/3 d); sandy loam (S 54; Si 34; C 12); find subangular blocky; friable; weakly cemented; plentiful roots; common pores; clear and smooth boundary; pH 7.4.
Btj	31 - 38 cm	Yellowish brown (10YR 5/4 d); sandy loam (S 54; Si 34; C 12) with fine sandy, reddish orange pockets and laminae *ca.* 1 cm in width; fine subangular blocky to single grain; firm to loose (m); strongly to weakly cemented; few roots and pores; clear and wavy boundary; pH 7.7.
Ck	> 38 cm	Brown (10YR 5/3 d); sandy loam (S 52; Si 38; C 10); fine subangular blocky; firm; weakly cemented; few roots and pores; pH 7.7.

This soil type shows no evidence of flooding. The presence of a well-developed soil profile, vegetation strata, and numerous flood-intolerant species indicates that the zone is and has been above the effects of inundation for a considerable time. The occurrence of orange pockets and laminae in the Btj horizon is probably the result of iron deposits as the prevailing groundwater level is well below the control section. Drainage and physiographic position appear to be important in soil and vegetation development in this section. This zone is controlled by autogenic

factors.

C. The Lake Athabasca Marsh Study Area

This area is dominated exclusively by the Gleyed Regosol Subgroup, with parent material consisting of recent water-sorted alluvium. Texturally, this parent material is loam and exhibits higher silt and clay contents than soils in the RC study area (App. 5). The pH values are generally alkaline (7.5-7.6) although a neutral class (7.1-7.2) is present (App. 5).

The Marsh Catena

Soils of this catena are stone free and exhibit either relatively constant or increasing pH values with profile depth. Soil types in this catena are closely and primarily related to low topography, restricted drainage, and high annual flooding susceptibility, and secondarily to vegetation. This catena is influenced entirely by allogenic factors.

1. The Immature Marsh Section

Gleyed Regosol was situated in a poorly to imperfectly drained and level, exposed, water-marsh transitional location at site #1, zone #51, under a *Salix interior-S. lutea/Typha latifolia* community.

Horizon	Thickness	Description Date - 10 October 71
Cg	0 - 25 cm	Pale brown (10YR 5/3 d) to brown (10YR 6/3 d) with bluish laminae *ca.* 1 cm in width occurring at 1, 5, 13, and 15 cm; loam (S 48; Si 34; C 18); amorphous; friable; weakly cemented; plentiful roots; common pores; clear and smooth boundary; pH 7.2.
Cg_1	> 25 cm	Pale brown (10YR 5/3 d) to brown (10YR 6/3 d) with orange and blue mottles occurring throughout; loam (S 48; Si 33; C 19); amorphous; friable; weakly cemented; few roots and pores; pH 7.3.

This soil profile lacks an LFH layer and has oxidation-reduction bands in the upper and mottling in the lower layers. These properties suggest that the soil is currently subjected to intense but short intervals of annual flooding with long drawdown periods having fluctuating water levels. This soil also has a loam texture and relatively constant sediment composition and pH values throughout the profile, indicating that flooding and its effects have been relatively uniform over a long period. This soil appears to be primarily controlled by flooding and secondarily by topography and drainage. Species in this zone are well-adapted to flooding and its effects but do not appear to influence soil development other than by sediment entrapment and stabilization.

2. The Marsh Section

2a. The Ah Horizon Subsection

Gleyed Regosol was situated in a poorly to imperfectly drained and level location at site #1, zone #53,

under a *Salix lutea/Eleocharis palustris* community.

Horizon	Thickness	Description Date - 10 October 71
L,H	trace	Light yellowish brown (10YR 6/4 d) to yellowish brown (10YR 5/4 d) semi-decomposed deciduous and graminoid litter; pH 7.4.
Ah	trace	Brown (10YR 5/3 d); loam (S 48; Si 35; C 17); amorphous; friable; weakly cemented; abundant roots; few pores; clear and smooth boundary; pH 7.5.
Cg	0 - 33 cm	Pale brown (10YR 6/3 d) to brown (10YR 5/3 d) with numerous orange and blue alternating laminae; loam (S 50; Si 33; C 17) amorphous; friable; weakly cemented; plentiful roots; common pores; clear and smooth boundary; pH 7.5.
Cg_1	> 33 cm	Pale brown (10YR 6/3 d) to brown (10YR 5/3 d) with predominantly bluish mottles; loam (S 50; Si 32; C 18); amorphous; very friable; weakly cemented; plentiful roots; common pores; pH 7.6.

This soil profile, in contrast to the previous one, has an initial L,H layer and Ah horizon. It is characterized by numerous mottles and oxidation-reduction bands, by increasing pH values with depth, and by relatively constant sand, silt, and clay contents. These properties suggest that flooding and its effects have been relatively uniform over a long period but not as severe as in the previous section. Although the vascular species are flood tolerant, the presence of mosses indicates that sedimentation is not as active as in the preceding section. Drainage, topography, and vegetation have become increasingly more important in influencing soil development in this zone.

2b. The L,H Layer Subsection

Gleyed Regosol was situated in an imperfectly drained and level location at site #1, zone #56, under a *Salix bebbiana/S. interior/Carex atherodes* community.

Horizon	Thickness	Description Date - 10 October 71
L,H	trace	Pale brown (10YR 6/3 d) to brown (10YR 5/3 d) semi-decomposed deciduous and graminoid litter; pH 7.6.
Cg	0 - 53 cm	Pale brown (10YR 6/3 d) to brown (10YR 5/3 d) with numerous orange and blue alternating laminae and layers with major bluish bands occurring at 15, 19, 22, 28, and 36 cm; sandy clay loam to loam (S 52; Si 28; C 20); amorphous; friable; weakly cemented; abundant roots; common pores; pH 7.6.

This soil profile has an L,H layer but lacks an initial Ah horizon of the previous subsection. Oxidation-reduction bands occur throughout the profile but mottling is totally lacking, suggesting that annual flooding and lack of a suitable drawdown period are sufficient to inhibit soil development. The high clay content probably resulted from selective over-levee sorting and from entrapment by flood tolerant vegetation. The presence of mosses indicates that sedimentation is not as active as in the previous section. Flooding and drainage are still major factors influencing soil development while topography and vegetation are less important.

D. The Chilaway Snye Study Area

Parent materials consist mostly of recent water-sorted alluvium. Texturally, they are mostly clays with some sandy loams, sandy clays, loamy sands, sandy clay loams and sands present (App. 6). The highest clay content occurs in this study area and is an important factor affecting drainage and vegetation patterns. The pH values are generally acidic (5.6-6.5) but some are neutral (6.7-7.1) and alkaline (8.3; App. 6).

The Marsh-Upland Catena

Soils of this catena are mostly stone free and generally exhibit increasing pH values with profile depth. Soil development is closely related to increasing influence of the vegetation, increasing height above MSWL's, improving drainage conditions, and decreasing flooding effects. This catena is under the influence of allogenic, polygenic, and autogenic factors.

1. The Marsh Section

Rego Gleysol was situated in an imperfectly drained and level location at site #1, zone #78 under a *Salix pyrifolia-S. lutea/S. lutea-Mentha arvensis-Carex atherodes* community.

Horizon	Thickness	Description Date - 18 June 71
L,H	1 - 0 cm	Pale yellow (2.5Y 7/4 d) semi-decomposed deciduous, herbaceous, and moss litter; pH 6.0.
Ah	0 - 5 cm	Dark grayish brown (10YR 4/2 d); clay (S 41; Si 14; C 45); very fine subangular blocky; firm; strongly cemented; plentiful roots; common pores; clear and smooth boundary; pH 5.8.
Cg	5 - 61 cm	Grayish brown (10YR 5/2 d) to brown (10YR 5/3 d) with orange mottles (10%) above and blue mottles (5%) below 18 cm; clay (S 41; Si 15; C 44); very fine subangular blocky; firm; strongly cemented; plentiful roots; common pores; pH 6.5.

This soil profile has an LFH layer and Ah horizon, indicating the absence of severe annual flooding and its effects. The relatively constant sediment composition of this profile reflects the uniformity of the suspended loads in flood waters. The high clay concentrations from flooding provide an impermeable lining retaining flood waters and restricting drainage which, in turn, affect soil development and species abundance. The presence of mottling indicates the influence of annual drawdown periods. Species in this zone have contributed to soil development by the entrapment of sediments. The vegetation's decomposition products seem to lower pH values. This zone appears to be controlled by allogenic factors.

2. The Meadow Section

Rego Gleysol was situated in an imperfectly drained and level location at site #1, zone #80, under a *Salix lutea-S. petiolaris/Carex atherodes* community.

Horizon	Thickness	Description Date - 18 June 71
LFH	2 - 0 cm	Brown (10YR 5/3 d) semi-decomposed deciduous, graminoid, and moss litter; pH 6.0.
Ah	0 - 8 cm	Dark grayish brown (10YR 4/2 d); clay (S 42; Si 14; C 44); very fine subangular blocky; firm; strongly cemented; abundant roots; common pores; gradual and smooth boundary; pH 6.3.
Cg	8 - 61 cm	Grayish brown (10YR 5/2 d) with orange mottles (50%) above and blue mottles (30%) below 25 cm; clay (S 41; Si 13; C 46); very fine subangular blocky; firm; strongly cemented; plentiful roots; common pores; pH 6.7.

This soil profile does not differ greatly from that in the preceding section. However, soil development is influenced by poor drainage and fluctuations in groundwater levels which inhibit the expression of Ae and Bt horizons. Topographic position is becoming more an important factor as this zone is affected only by over-levee floods. During periodic floods, species in this zone contribute to soil development by entrapment of sediments. The vegetation's decomposition products seem to lower pH values. This zone appears to be controlled by polygenic factors.

3. The Fen-Upland Section

Orthic Gleysol was situated in a moderately well-drained and gently sloping location at site #1, zone #83, under a *Salix bebbiana/S. arbusculoides/Equisetum pratense* community.

Horizon	Thickness	Description Date - 23 June 71
LFH	2 - 0 cm	Very dark grayish brown (10YR 3/2 d) deciduous leaf litter; pH 5.8.
Ah	0 - 5 cm	Dark grayish brown (10YR 4/2 d); sandy clay (S 46; Si 8; C 46); granular; loose (m); weakly cemented; plentiful roots; common pores; clear and smooth boundary; pH 5.6.
Aejg	5 - 25 cm	Grayish brown (10YR 5/2 d) with red mottles (25%) throughout; sandy clay (S 49; Si 11; C 40); fine subangular blocky; slightly firm; strongly cemented; plentiful roots; common pores; clear and smooth boundary; pH 5.9.
Bgtj	25 - 65 cm	Yellowish brown (10YR 5/4 d) with red mottles (50%) throughout; sandy loam (S 72; Si 17; C 11); fine subangular blocky; loose (m); weakly cemented; few roots and pores; clear and smooth boundary; pH 6.3.
$Bgtj_1$	65 - 85 cm	Light yellowish brown (10YR 6/4 d) with red mottles (20%) and grayish clay laminae throughout; loamy sand (S 78; Si 17; C 5); single grain; loose (m); weakly cemented; few roots and pores; few stones (8 cm in diameter); clear and smooth boundary; pH 6.4.
Cca	> 85 cm	White (10YR 8/1 d); sandy clay loam (S 68; Si 9; C 23); fine subangular blocky; firm; strongly cemented; few roots and pores; few stones (8 cm in diameter); pH 7.1.

This soil, with Aejg and Bgtj horizons, has a better developed profile than the preceding soils of this catena. The clay content decreases throughout the profile except for the lowest horizon which is characterized by stones and relatively high clay content. The solum exhibits increasing pH values with depth. These characteristics suggest that flooding had been previously significant in the development of the soil profile. However, recent periodic flooding effects in this zone are not as noticeable because of increased height above MSWL. When flooded, this zone is also adequately drained because of the relatively high sand content throughout the profile. The presence of red mottling in Bgtj horizons is probably the result of iron deposits, exhibited as bands and nodules, rather than fluctuations in the prevailing groundwater level which is well below the control section. This zone is controlled by polygenic factors.

4. The Upland Section

Fera Gleysol was situated in a moderately well-drained and gently sloping location at site #1, zone #84, under a *Populus tremuloides-Betula papyrifera/ Amelanchier alnifolia/Pyrola asarifolia* community.

Horizon	Thickness	Description Date - 19 June 71
LFH	5 - 0 cm	Dark brown (10YR 3/3 d) to brown (10YR 5/3 d) deciduous leaf litter; pH 6.3.
Ah	0 - 8 cm	Dark brown (10YR 4/3 d) to dark yellowish brown (10YR 4/4 d); sandy loam (S 58; Si 34; C 8); very fine single

Ah (cont'd)		grain; loose (m); weakly cemented; plentiful roots; common pores; gradual and smooth boundary; pH 7.1.
Bgf	8 - 74 cm	Yellowish brown (10YR 5/6 d) with orange mottles (10%) and numerous orange horizontal laminae; sandy loam (S 73; Si 21; C 6); amorphous to single grain; loose (m); weakly cemented; plentiful roots; common pores; clear and smooth boundary; pH 7.0.
Ck	> 74 cm	Yellowish brown (10YR 5/4 d) to brown (10YR 5/3 d); fine sand (S 89; Si 8; C 3); fine single grain; loose (m); weakly cemented; few roots and pores; pH 8.3.

Classification of this profile is tentative. It differs from the preceding one by lacking Aejg and Bgtj horizons and by having a Bgf horizon. The presence of flood-intolerant species in well-developed strata indicates that the zone is and has been above the effects of flooding for a considerable time. The occurrence of orange mottling and laminae in the Bgf horizon is probably the result of iron deposits as the prevailing groundwater level is well below the control section. Drainage and topographic position appear to be important in soil and vegetation development in this section. This zone is controlled by autogenic factors.

E. The Egg Lake Study Area

This area has parent materials consisting of recent water-sorted alluvium. Texturally, the soils are predominantly sandy loams with some loams present. The pH

values are generally neutral (6.7-7.4) but some are acidic (5.5-6.4) and alkaline (8.0-8.3; App. 7). Numerous buried organic layers occur in all profiles with some mottling also present.

The Meadow-Upland Catena

Soils of this catena are stone-free, and generally show increasing pH values with profile depth. Soil development is related to increasing height above MSWL's, improving drainage conditions, decreasing flooding effects, and vegetation. This catena is controlled by polygenic and autogenic factors.

1. The Meadow Section

The Orthic Gleysol soils were not described in any detail compared to other soil types because the water levels in the zones were just at or below the surface. Soils belonging to this Order had very numerous alternating Ahb layers and Aejg horizons followed, in some cases, by a Bg horizon. These soils have similar characteristics as those in the following section. The meadow zones are controlled by polygenic factors.

2. The Fen Section

Orthic Gleysol was situated in a poorly drained and slightly higher location at site #2, zone #118, under a *Salix bebbiana/Carex atherodes* community.

Horizon	Thickness	Description Date - 7 July 71
LFH	5 - 0 cm	Dark brown (10YR 3/3 d) semi-decomposed deciduous and graminoid litter; pH 6.1.
Ah	0 - 5 cm	Dark reddish brown (5YR 2.5/2 d); loam (S 49; Si 35; C 16); single grain; friable; weakly cemented; abundant roots; many pores; abrupt and smooth boundary; pH 5.5.
Aeg	5 - 23 cm	Light gray (10YR 7/1 d) with blue mottles (50%) throughout; sandy loam (S 57; Si 34; C 9); subangular blocky; firm; strongly cemented; plentiful roots; common pores; clear and smooth boundary; pH 6.2.
Ahb	23 - 27 cm	Dark reddish brown (5YR 2.5/2 d); pH 6.9.
Aeg_1	27 - 30 cm	See Aeg (few roots).
Ahb_1	30 - 34 cm	See Ahb.
Aeg_2	34 - 36 cm	See Aeg (few roots).
Bg	36 - 56 cm	Pale brown (10YR 6/3 d) with blue mottles (50%) throughout; sandy loam (S 54; Si 32; C 14); subangular blocky; friable; weakly cemented; few roots and pores; clear and smooth boundary; pH 6.9.
Ahb_2	56 - 57 cm	See Ahb.
Aeg_3	57 - 80 cm	See Aeg; pH 7.4 (very few roots).
Bg_1	> 80 cm	See Bg; pH 7.4 (very few roots).

This soil profile differs from the last in having Aeg horizons and fewer buried organic layers. These soil characteristics suggest that this zone was influenced by fewer floods at longer intervals. This soil profile appears to have had alternating flooding and non-flooding periods of varying durations. During latter periods,

there was either sufficient time for the development of Aeg horizons or more than sufficient time for the occurrence of Bg horizons. In both developmental situations, reflooding permitted gleying of the newly formed horizons. There is a general increase in pH values with depth, probably resulting from the influence of vegetation, parent materials, and groundwaters. Sandy loams occur throughout the profile which may be indicative of similar long-term over-levee suspended load composition and sorting during soil development. Zonal species composition appears to be well adjusted to relatively long periods of flooding and non-flooding. Polygenic factors control this zone.

3. The Upland Section

Cumulic Orthic Gray Luvisol was situated in a well-drained and very gently sloping location at site #2, zone #120, under a *Populus balsamifera/Rosa acicularis-Viburnum edule/V. edule* community.

Horizon	Thickness	Description Date - 7 July 71
LFH	8 - 0 cm	Dark reddish brown (5YR 2.5/2 d); semi-decomposed deciduous leaf litter; pH 6.6.
Ah	0 - 5 cm	Very dark brown (7.5YR 2.5/2 d); sandy loam (S 70; Si 24; C 6); single grain; friable; weakly cemented; abundant roots; common pores; gradual and smooth boundary; pH 6.7.
Ae	5 - 15 cm	Brown (10YR 5/3 d); sandy loam (S 58; Si 34; C 8); single grain; loose (m); weakly cemented; plentiful roots;

Ae (cont'd)		common pores; clear and smooth boundary; pH 7.2.
Btj	15 - 31 cm	Dark brown (10YR 3/3 d); sandy loam (S 56; Si 34; C 10); subangular blocky; friable; weakly cemented; plentiful roots; common pores; clear and wavy boundary; pH 8.0.
Bt	31 - 33 cm	Brown (7.5YR 5/4 d); sandy loam (S 54; Si 34; C 12); subangular blocky; friable; weakly cemented; few roots and pores; abrupt and wavy boundary; pH 8.2.
Ahb	33 - 34 cm	Black (10YR 2.5/1 d).
Ck	34 - 46 cm	Brown (10YR 5/3 d); sandy loam (S 70; Si 24; C 6); subangular blocky; friable; weakly cemented; few roots and pores; clear and smooth boundary; pH 8.3.
Ahb_1	46 - 47 cm	See Ahb.
Ck_1	47 - 48 cm	See Ck (very few roots in remaining horizons).
Ahb_2	48 - 50 cm	See Ahb.
Ck_2	50 - 86 cm	See Ck.
Ahb_3	86 - 88 cm	See Ahb.
Ck_3	> 88 cm	See Ck.

The presence of sandy loam throughout the profile suggests uniformity in over-levee sediment loads in flood waters while alternating Ahb layers and Ck horizons in the lower portion of the profile indicate past variations in alternating flooding and non-flooding periods. The development of distinct Ae and Bt horizons suggests that the zone has not been influenced by the same flood waters affecting the previous sections. Mottling and gleying are

completely absent from the profile, indicating that re-flooding has not occurred recently and that a fluctuating groundwater table is located well below the control section. The absence of any flooding is reflected in flood-intolerant species in well developed strata. This zone is presently controlled by autogenic factors.

F. The Nuphar Lake Study Area

This area has soils belonging to Organic and Luvisolic Orders. The parent material for the latter is glacial till overlying Precambrian outcrop. Physical and chemical soil properties are given in Appendix 8.

The Bog-Upland Catena

1. The Bog Section

Organic soils were not described in any detail compared to other soil types because the water levels at site #1 were just at or below the peat surface. Soils belonging to this Order have two distinctive and diagnostic layers. Approximately 85% of the bog has a hydric layer and is recognized as a floating bog; the remaining 15% has a cryic layer designated as a hummocky bog. The peat is stone- and sediment-free, and exhibits decreasing pH values with depth. These values are acidic (5.0-5.5). Isolated physiographic position, poor and restricted drainage, stable water level, and absence of flooding and its effects are among the factors

contributing to the development of *Sphagnum* spp., and consequently organic soils. The relatively ombrotrophic bog zones are controlled by autogenic factors.

2. The Upland Section

Orthic Gray Luvisol was situated in a moderately well-drained and gently sloping location at site #1, zone #137, under a *Populus tremuloides-Picea glauca/Viburnum edule/V. edule-Rosa acicularis* community.

Horizon	Thickness	Description Date - 19 August 71
L-H	1 - 0 cm	Black (10YR 2.5/1 d) semi-decomposed deciduous and coniferous litter; pH 6.5.
Ah	0 - 4 cm	Black (5YR 2.5/1 d); loam; loose (m); weakly cemented; abundant roots; many pores; clear and smooth boundary; pH 5.9.
Ae	4 - 9 cm	Very pale brown (10YR 7/3 d); sandy loam (S 60; Si 22; C 18); subangular blocky; loose (m); weakly cemented; plentiful roots; few pores; gradual and smooth boundary; pH 6.4.
AB	9 - 15 cm	Pale brown (10YR 6/3 d); sandy loam (S 58; Si 24; C 18); amorphous; firm; strongly cemented; few roots and pores; gradual and smooth boundary; pH 6.3.
Bt	15 - 67 cm	Light yellowish brown (10YR 6/4 d) with greenish-white laminae throughout; clay (S 44; Si 10; C 46); subangular; blocky; hard (d); strongly cemented; very few roots and pores; clear and smooth boundary; pH 5.7.
Bt_1	67 - 69 cm	Very pale brown (10YR 7/3 d); sandy clay (S 46; Si 18; C 36); subangular blocky; loose (m); weakly cemented; abrupt and irregular boundary; pH 5.6.

Bt_2	69 - 90 cm	Light yellowish brown (10YR 6/4 d) with four grayish-green laminae per each 2.5 cm; sandy clay loam (S 52; Si 14; C 34); subangular blocky; very hard (d); strongly cemented; very few roots and pores; clear and smooth boundary; pH 5.4.
C	90 - 94 cm	Pink (7.5YR 7/4 d); sand (S 97; Si 1; C 2); single grain; loose (m); weakly cemented; few to abundant, and medium to large stones; clear and smooth boundary; pH 5.8.
R	> 94 cm	Precambrian rock.

Classification of this soil type is tentative. The laminae in Bt horizons are probably peri-glacial outwash or lacustrine varves. The soil profile has no stones except in the very thin till cap overlying the Precambrian outcrop. The acidic nature of the soil is a reflection of the parent materials and vegetation decomposition products. Acidic parent materials, high topographic position, good drainage, and absence of flooding appear to be important factors in the development of this profile. This zone is controlled by autogenic factors.

G. Synthesis

For much of the study region, sand and silt increase with depth, presumably because of the gradual increase in elevation as alluvial deposits build up. The pH values generally increase with depth, probably resulting from the influence of vegetation, alluvial parent materials, and groundwaters.

The soils within and among study areas generally reflect interactions of different geomorphological and successional processes. Varying intensities and rates of flooding and sedimentation affect primarily the physical soil properties and also the environment, which is in turn reflected in the flora and vegetation patterns. With sufficient sediment build-up, allogenic factors decrease in importance while autogenic factors increase their influence changing edaphic properties, environmental factors, and vegetation attributes. Eventually, amelioration of the environment permits only the operation of autogenic factors. Under the total influence of autogenic factors, the soil and vegetation begin to develop in conjunction with each other to a state of dynamic equilibrium, barring disturbances such as fire. In the study region the soil catena stages closely correspond to vegetation seral stages. This relationship has been previously observed by Mirkin and Miftakhov (1963) in the floodplain of the Belaya River. The modification of the environment through increasing height above MSWL, improving drainage, increasing physiographic control and substrate stability, decreasing flooding effects, and vegetation control, among others, is reflected in the different soil types.

LITERATURE REVIEW

I VEGETATION

Historically, numerous explorers, travellers, and scientific investigators have written about the complexity of the vegetation and the regularity of its pattern in the PA Delta (Fuller & La Roi 1971).

According to Halliday (1937) the PA delta lies within the Mackenzie Lowlands Section (B.23) of the Boreal Forest Region. This section is essentially characterized by forests of wide extent composed of a *Picea glauca* Association occurring on higher levee areas, by forests of a smaller extent having a prominent *Populus balsamifera* Association along river banks, and by forests of very limited extent of a *Pinus banksiana* Association located on light soils and on rock outcrops. These species exhibit excellent growth in rapidly drained areas. The more poorly drained depressions behind levee areas support *Picea mariana* and *Larix laricina* bogs and muskegs, with flatter areas having meadows and *Salix* scrub.

The Boreal Forest (Northern Coniferous) Phytogeographic Region of Moss (1955) corresponds to Mixedwood (B.18), Northern Coniferous (B.22), and Mackenzie Lowlands (B.23) Sections of Halliday's classification. The *Picea glauca* Association of Moss (1955) has three divisions of

which only the Floodplain Type has any importance in the study region. This type has open *P. glauca* stands composed of minor amounts of *Populus balsamifera* and *Salix bebbiana*, and a prominent shrub stratum having *Viburnum edule*, *Ribes* spp., and *Rosa* spp., and also a luxuriant herb stratum with *Linnaea borealis*, *Rubus pubescens*, and *Mertensia paniculata* among others. The three types had been intensively treated earlier by Raup (1946).

The *Pinus banksiana* Consociation of the *P. banksiana-Pinus contorta* Association of Moss (1955) occurs in the study region. Within this consociation only the Pine-Heath Faciation is recognized as being important. This faciation occurs on dry and open locations and is characterized by *Arctostaphylos uva-ursi*, *Vaccinium vitis-idaea*, *Elymus innovatus*, and *Polytrichum* and *Cladonia* spp. This consociation had been previously treated in detail by Raup (1946).

The *Picea mariana* Associations of Moss (1955) are composed of two main types. The *P. mariana-Hylocomium splendens* type, having little peat accumulation, occurs in shallow depressions and on level areas which have progressed through sedge, grass, and willow stages. This type is interpreted by Moss (1953a) as an edaphic climax because of poor drainage and periodic burning. The *P. mariana-Sphagnum* type is characterized by *Larix laricina*, *Betula papyrifera*, *Salix* spp.; by *Ledum*

groenlandicum and *Vaccinium vitis-idaea*; by *Rubus chamaemorus* and *Smilacina trifoliata*; and by *Sphagnum* and *Cladonia* spp. This type is located in depressions having proceeded through numerous bog stages resulting in a large accumulation of sphagnum peat. This type is interpreted by Moss (1953a) as a subclimax stage of a bog forest sere maintained by edaphic conditions and periodic burnings. This type may be succeeded by the *P. mariana-H. splendens* type (Moss 1955).

The *Larix laricina* Association is similar to the *Picea mariana-Sphagnum* type in being developed on a peaty substratum. Moss (1953a) interpreted this association as a subclimax stage of a bog forest sere where *Larix*, established in a *Drepanocladus-Carex-Betula* bog, continues to maintain the relatively wet bog conditions. The *L. laricina* Association may be succeeded by the *P. mariana-Sphagnum* type (Moss 1955). *Picea mariana* is often interspersed among the dominant *L. laricina*. The understory is composed of *Betula*, *Salix*, and *Vaccinium* shrub species, and *Caltha palustris*, *Potentilla palustris*, and *Carex* spp. with *Aulacomnium*, *Drepanocladus*, and *Sphagnum* species covering a hummocky terrain. Raup (1946) had previously treated, as Bog Forests, the *P. mariana* and *L. laricina* Associations of Moss (1953a).

The vegetation mosaic present in the PA delta is representative of the Upper Mackenzie Section (B.23a) of

the Boreal Forest Region of Rowe (1959, 1972). As recognized by Rowe, the deltaic vegetation consists broadly of stream levee, marsh, meadow, fen, and bog types.

The first comprehensive research was conducted by Raup (1935) who made a botanical and subjective ecological survey of the flora and vegetation, and described some of the more common successional sequences in Wood Buffalo National Park. Within the deltaic section of the park he recognized, based on physiographic-physiognomic criteria, seven main vegetation types as follows: Aquatic, Shore, Herbaceous, Meadow, Shrub, Tree, and Outcrop Associations. Other studies by Raup (1930, 1933, 1936, 1946) provide a comprehensive understanding of vegetation patterns existing in the PA delta and surrounding region.

Several studies have been completed on the ecology of the PA delta by Dirschl (1970a, 1971, 1972, 1973). His work was concentrated in the southwestern portion of the delta and focused on short- and long-term vegetation adjustments and successional patterns resulting from effects of low water levels. The following five basic community types based on physiographic-physiognomic criteria were recognized: Aquatic (open water), Shore (emergents, mudflats, and immature fen), Meadow (*Carex* and *Calamagrostis* meadows), Shrub (low and tall shrubs), and Forest (deciduous and coniferous forests). Dabbs (1971) and Dirschl *et al.* (1974), using

physiographic-physiognomic criteria, mapped and classified the deltaic vegetation on a small scale into essentially seven aquatic and eight terrestrial community types. These latter types were: Immature Fen, Fen, Low Shrub, Tall Shrub, Deciduous Forest, Coniferous Forest, Precambrian Outcrop Grassland, and Precambrian Outcrop Forest. Relationships of these types and their corresponding dominant species were made to moisture and edaphic properties. Townsend (1973b), in preparing a vegetation map of the PA delta, recognized 11 major habitat types as follows: Water, Emergents, Mudflat, Immature Fen (meadow), Sedge Meadow, Grass Meadow, Low Shrub, Tall Shrub, Deciduous Trees, Coniferous Trees, and Rock Outcrop. He suggested that these habitat types have been stratified along a topographic gradient according to long-term, water-level fluctuations and plant succession.

Comparison of similar ecological studies undertaken in other Canadian deltaic and wetland regions can provide pertinent supporting information to this study and place the PA delta region in perspective in relation to the remainder of western and northern Canada. In the Cumberland Marshes of the Saskatchewan River delta, Dirschl (1970b) and Dirschl and Coupland (1972) recognized 11 basic vegetation types according to physiognomic criteria. The distributions of species and communities were controlled by moisture regime, nutrient status, and pH

values. The vegetation types and their controlling environmental factors appear to be identical to those observed by Dirschl in the PA delta. However, the Saskatchewan delta, unlike the PA delta, is located in a more temperate setting which has had less drastic water-level fluctuations resulting in more extensive, stable, deltaic, vegetation types (Dirschl *et al.* 1974).

Studies by Walker (1959, 1965) in the delta marshes of southern Lake Manitoba revealed that floristic and vegetation patterns were controlled by depth and duration of floodwaters, and by physical and chemical soil properties. Species colonization patterns similar to those reported by Walker were observed in the PA delta by Dirschl (1970a, 1971, 1972, 1973).

In the Mackenzie delta, N.W.T., Gill (1971) recognized 10 terrestrial associations using floristic criteria, and gave subsidiary notes on aquatic associations and secondary plant succession. Among factors controlling the distribution of flora and vegetation, flooding effects, topography, soil properties, and permafrost were the major contributors. Except for permafrost, these factors are also important in controlling flora and vegetation patterns in the PA delta (Dirschl 1973).

In a study of forest types along the lower Liard River, N.W.T., Jeffrey (1961, 1964) recognized seven landscape units and 55 ecosystem types which were based

on physiographic-vegetational criteria. In each ecosystem the topography, soil, forest cover, and lesser vegetation were described. His 13 ecosystem types of the Recent Floodplain Landscape Unit are similar to the riparian vegetation types recognized in the PA delta by Dirschl *et al.* (1974).

Major wetland vegetation types (marshes, wet and dry meadows, bogs, and muskegs) observed in the delta region by Raup (1935) have also been examined by Lewis and Dowding (1926) and Lewis *et al.* (1928) in central Alberta, and by Moss (1952, 1953a,b) in western and northwestern Alberta. Comparative studies on environmental-vegetation relationships observed by Dirschl *et al.* (1974) in the PA delta were earlier examined by Walker and Coupland (1968) and Walker and Wehrhahn (1971) in the wetlands of Saskatchewan. In these investigations of deltaic, riparian, and wetland regions, the authors have shown the importance of seasonal inundation and drawdown, sediment deposition and erosion, nutrient availability, and topography in controlling the distribution of flora and vegetation.

II PLANT SUCCESSION

Plant succession is an orderly, directional, and predictable process of community development which involves changes in species structure and community

processes with time, resulting in community modification of the environment and, eventually, a relatively stable ecosystem (Odum 1971). The flora and vegetation patterns in the delta, having developed during the last 10,000 years, show predictable alignments according to topography and moisture regime in adjusting to annual spring and summer floodings. During the past 300 years, these flora and vegetation patterns have changed little (Fuller & La Roi 1971). For example, re-examination by Dabbs (1971) of a transect originally made by Raup (1935) in a very active portion of the delta revealed that, although *Calamagrostis canadensis* had replaced *Carex atherodes* and in some cases *Salix* spp. had become established, the same species and vegetation types were present and aligned in a similar progression according to topographic and moisture gradients on both occasions.

Deltaic succession is quite complex and consists of numerous branching pathways in which various species groups dominate in different locations during the same seral stages in wetland community types and converge during later stages toward upland communities. These pathways are illustrated in a successional diagram presented by Raup (1935:88) who presented an outline of plant succession for major species and vegetation types in the Mackenzie Lowlands. He indicated the general trend of succession from lowland to upland areas in regions

created by different physiographic processes. His major hydrarch sequence may be summarized as follows: *Nuphar-Potamogeton-Sparganium-Myriophyllum-Sagittaria-Ranunculus* species mixtures → *Potamogeton-Typha-Scirpus-Glyceria-Beckmannia-Carex-Calamagrostis* species mixtures → *Equisetum-Salix* species mixtures → *Salix-Alnus-Populus* species mixtures → *Populus-Picea* species mixtures → *Picea glauca*.

Dirschl (1972:60) and Dirschl *et al.* (1974:30) modified Raup's successional sequences to incorporate, to a much greater degree, long-term successional processes that operate in the PA delta. Major species and community types were positioned in relation to geomorphological processes in which there is a nutrient decrease from active, to semi-active, to inactive deltaic regions. In both diagrams, the bog successional sequence having *Salix pedicellaris* → *Menyanthes trifoliata* → Hypnic Mosses → *Sphagnum* spp. → *Ledum-Kalmia-Andromeda* → *Picea mariana*, *Larix laricina* was earlier described in detail by M. S. Moss (1949) and E. H. Moss (1953b) for Alberta and northwestern Alberta respectively.

Moss (1953b) observed two main bog series. The *Drepanocladus-Carex* bog series, taking place in open basins, had the following sequence: aquatic → marsh → bog willow and birch → *Larix* or *Sphagnum-Ledum-Picea* stages. The second series (*Sphagnum* bog) appeared to be more

prevalent and had developed directly from aquatic and marsh vegetation types. The typical bog sequence of closed basins, as described by M. S. Moss (1949) and E. H. Moss (1953b), is from wet conditions having *Sphagnum subsecundum* (or *S. teres*) → *S. recurvum* → *S. magellanicum* → *S. capillaceum* → *S. fuscum* → *Polytrichum* spp. → *Cladonia* spp. in dry conditions. The corresponding sequence for vascular species is *Andromeda polifolia* → *Rubus chamaemorus* → *Oxycoccus microcarpus* → *Vaccinium vitis-idaea* → *Ledum groenlandicum* → *Eriophorum spissum*. The last stage in both sequences is the bog forest. The same species in these sequences are present in corresponding stages of the regeneration cycle in which the above species replacements take place as hollows having hygrophilous species proceed to mounds having less hygrophilous species which in turn degenerate to hollows. Eventually, a state of dynamic equilibrium is reached when the general bog surface becomes too dry for any *Sphagnum* species except *S. fuscum*. The above *Sphagnum* sequence is common in large, wet depressions and in marsh or hypnic bog types where *Sphagnum* is advancing. Thus, the general bog appearance is a species mosaic related to variations in microtopography and moisture regime (Moss 1953b).

Moss (1953b) also recognized a general wetland successional sequence involving aquatic → reed swamp → marsh → wet meadow → wooded communities. He suggested

that the sequence may be maintained indefinitely at the meadow stage because of heavy, poorly aerated, alluvial soils having compact surface and high plant cover which, in addition to periodic flooding, may prevent invasion of tree species.

Horton (1965:48) showed, for the lower Peace River, the arrangement of associations with corresponding dominant species along a schematic topographic profile from recent alluvial to "non-alluvial" upland areas. Within each association he indicated productivity status, moisture regime, and major successional trends. Horton (1965) proposed, and Blyth (1965) substantiated, that all forest associations on alluvial and non-alluvial areas of new and old deltas along the lower Peace River are subject to and maintained by fires. He emphasized that most associations, including those in lowland areas (*e.g.*, Floodplain *Picea glauca* Forests), have a fire origin and that fire, not flooding, is the main factor initiating succession. According to Horton, fire usually occurs before a sere can reach the *P. glauca* stage, resulting in a return to *Salix*, *Alnus*, and *Populus* scrub with a *Picea* understory. Raup (1946) reported that, in the Floodplain *P. glauca* Forests, fire does occur but *P. glauca* is capable of regeneration to form pure stands. However, he noted that fire is prevalent in Upland Mesophytic *P. glauca* Forests and has greatly altered the character of these forests by

retrogression to poplars and pine, producing three basic modifications depending upon fire intensities and soil types. He observed that repeated fires will maintain these forests at these stages, but lack of fire will eventually allow the return of the forests to *P. glauca*. Jeffrey (1964) supported Raup's viewpoint by emphasizing that fire is the most important factor in older floodplains, while flooding is the major environmental factor creating disturbance in recent floodplain vegetation types. Horton's interpretation of the development of some of his associations, specifically more recent Floodplain *P. glauca* Forests, to fire and not flooding is controversial.

Occurrences of fire in bog communities have been described by Lewis *et al.* (1928) for *Ledum* moor, Raup (1946) for the wet bog forest type, and Moss (1953b) for the Black Spruce-Feather Moss Association. They concluded that repeated burning maintains bogs in early successional stages producing open, static bog stages existing under disclimax conditions. Moss (1953b) observed in northwestern Alberta that retrogression of wetland types, especially marsh, occurred through burning rather than flooding.

Jeffrey (1964:82) showed the following generalized vegetation trend along a topographic gradient on recent floodplain deposits of the lower Liard River: sandbar ⟶ *Salix* ⟶ *Salix-Alnus* ⟶ *Populus-Alnus* ⟶

Populus-Equisetum → *Populus-Picea-Equisetum* → *Picea-Populus* → *Picea-Betula*. Within this sequence he recognized forest types which were subject to disintegration and deterioration, and to successional alterations by insufficient *P. glauca* colonization. The prominent species in the successional sequence are similar to those in sequences observed in the PA delta by Raup (1935) and Dirschl *et al.* (1974).

Clements (1928) and Polunin (1960) consider the climax state to be achieved when a stand is composed of uneven-aged populations whose average lifespans are considerably shorter than the age of the stand itself. *Picea glauca* is considered to be the climatic climax species in northern Alberta by White (1915), Moss (1932, 1953a), Raup (1935, 1946), and Rowe (1953). Succession of poplar to white spruce is clearly indicated for northern Alberta by Moss (1955). These authors concluded that, when seed source is abundant and where appropriate ground conditions occur, establishment of *P. glauca* will take place. This species will then grow and extend its influence for many years under poplar stands, until thinning with advancing age creates openings in poplar canopies, allowing spruce to dominate over the poplar. The poplar is gradually replaced by pure stands of spruce which are self-perpetuating and in dynamic equilibrium with existing habitat factors. Although continual changes

take place and are necessary for the perpetuation of any community, drastic changes resulting from the introduction of pyric or hydrologic factors can produce definite temporal disequilibria that initiate new successional trends.

Kárpáti and Kárpáti (1962), Pen'kovskaya (1963), Barabash (1968), Kovacs (1968), and Kopecky (1969) observed that many species require regular and exact rhythms of environmental and biotic changes to stimulate new waves of regeneration. These waves allow optimal survival and perpetuation of flora and vegetation along restricted ranges of a topographic gradient. Becking (1968) had theoretically described responses of flora and vegetation to rhythmic and pulsating changes in biotic and environmental conditions. Although these changes in flora and vegetation resulting from annual water-level fluctuations have not been documented in the PA delta, the temporal intervals for successive replacement among different vegetation types have been indicated for long-term conditions of declining water levels and prolonged flooding by Townsend (1973a:032) using simulation model techniques. The number of growing seasons necessary for successive replacements to occur during a long-term decline in water levels was summarized by Dirschl (1973:J17) as follows: open water $\xrightarrow{\text{0 yrs}}$ exposed mudflat $\xrightarrow{\text{1 yrs}}$ immature fen $\xrightarrow{\text{3 yrs}}$ *Carex* meadow $\xrightarrow{\text{7 yrs}}$ *Calamagrostis* meadow $\xrightarrow{\text{10 yrs}}$ low willow shrub $\xrightarrow{\text{15 yrs}}$ tall willow shrub $\xrightarrow{\text{25 yrs}}$

deciduous forest $\xrightarrow{\text{50 yrs}}$ coniferous forest. Based on his findings, Dirschl (1973) suggested that succession proceeds rapidly in the initial stages, but becomes increasingly slower with each successive seral stage.

Gill (1971) suggested that within the Mackenzie Delta pioneer stages are controlled purely by allogenic factors, transitional stages by polygenic factors, and terminal stages by autogenic factors. Even though Gill found pioneer stages to be controlled wholly by allogenic factors, Daubenmire (1968) suggested that either completely autogenic or exclusively allogenic factors can initiate a sere. In his classification of the deltaic vegetation, Dirschl (1972) basically supported Daubenmire's suggestions, indicating that autogenic influences primarily operate in inactive geomorphological areas, while allogenic influences essentially occur in active and semi-active areas. Both Gill (1971) and Dirschl (1973) suggested that allogenic factors, predominantly flooding and sedimentation, change the environment forcing the direction of succession.

The previous authors have suggested that many different successional trends converge and are directed toward the climatic climax which is the most mesophytic and complex plant community present in a region. The previous authors implied that structural complexity, species diversity, biomass, and relative stability generally

increase during succession, with vegetation differences among areas being primarily the result of variations in zonal ages. Most of these authors concluded that the vegetation in riparian and floodplain regions is adapted to seasonal inundation such that wetland vegetation types can be maintained in their seral stages. However, changes in controlling factors which produce lower and more stable water levels, and subsequently restrict the influence of flooding, will permit normal successional sequences to continue. The previous authors observed that the flora and vegetation types are arranged in an orderly progression along an increasing relief gradient according to individual ecological requirements and tolerances, to biotic interactions, and to environmental controls. Positions along this gradient are maintained by an effective immigration, establishment, and competition. Some authors observed that herbaceous species were particularly sensitive to any deviation from the "norm" when certain controlling environmental factors combine in a specific habitat to create new conditions. Successional studies conducted in wetland areas of other regions support the conclusions of these investigators. The more pertinent studies are provided by Nielsen and Moyle (1941) and Moyle and Nielsen (1953) in northern Minnesota, Bliss and Cantlon (1957) in northern Alaska, Petty (1958) in Indiana, Gorchakovskii and Peshkova (1970) in U.S.S.R.,

Viereck (1970) in the interior of Alaska, and Lacoursière and Grandtner (1971) in Quebec.

RESULTS

I DESCRIPTION OF THE VEGETATION AND THE ENVIRONMENT

A. Floristics

The vascular flora of the study region is composed of 59 families, 160 genera, and 292 species (App. 9). The largest families in order of decreasing species numbers are Gramineae, Cyperaceae, and Compositae. This trend also prevails in other deltaic lowland regions. The flora in the study region is unique as a result of its geomorphological location; Precambrian outcrops contribute to this uniqueness because their habitats are much more stable and contain a blending of floral elements from the grassland and cordilleran regions. A comparison of species lists for the PA delta provided by Raup (1935), Gentle (1973), and this study reveal a progressive increase in our knowledge of the floristic composition of the delta. This study has added 21 vascular species not recorded previously in the delta (App. 9). The species diversity of the PA delta is richer than, and contrasts sharply with, those of non-deltaic areas in other parts of the boreal forest region.

B. Vegetation Units

In this study, "community types" (abstract units) composed of "communities" (concrete units) were used to categorize the vegetation (Whittaker 1967). The community types were viewed as occupying distinct positions along a vegetation gradient ("coenocline" of Whittaker 1967). A coenocline may be paralleled by a gradient of a single environmental factor ("factor gradient" of Whittaker 1967) or several environmental factors ("complex gradient" of Whittaker 1967). Together, the coenocline and complex gradients form an "ecocline" (Whittaker 1975). The coenocline can also be related to a time or successional gradient.

A "community type" is interpreted here as an abstract unit having more or less discrete and relatively uniform species assemblages which form communities consistent in structure and developmental history that exist in equilibrium with the existing complex of environmental and biotic factors. The extent and stability of a community type are controlled by either allogenic, autogenic, or polygenic influences. The degree of control exerted by these influences determines whether the unit will proceed to another community type or retrogress to a preceding one. Relatively distinct segregates within the community type are termed "subtypes". This thesis will place strong emphasis on the dynamic and successional

states of different community types present in the study region.

C. Vegetation Classification

Vascular species cover values were used in the cluster analysis. This analysis produced five dendrograms resulting from furthest neighbour, group average, minimum variance, nearest neighbour, and centroid clustering techniques. The minimum variance technique proved more effective than the others. The author grouped 165 communities into 16 community types and determined the six subtypes using physiognomic and floristic criteria (Fig. 2). Dendrograms arising from the last two techniques, though not differing greatly from the others, were not used for interpretation because they did not contain sufficient subordinate clusters. Pritchard and Anderson (1971) and Achuff and La Roi (1977) also found the first three techniques to be useful in vegetation analysis, with the minimum variance being the best. The final placement of communities was based on physiognomic and floristic criteria. The minimum number of communities allowed to form a community type was three.

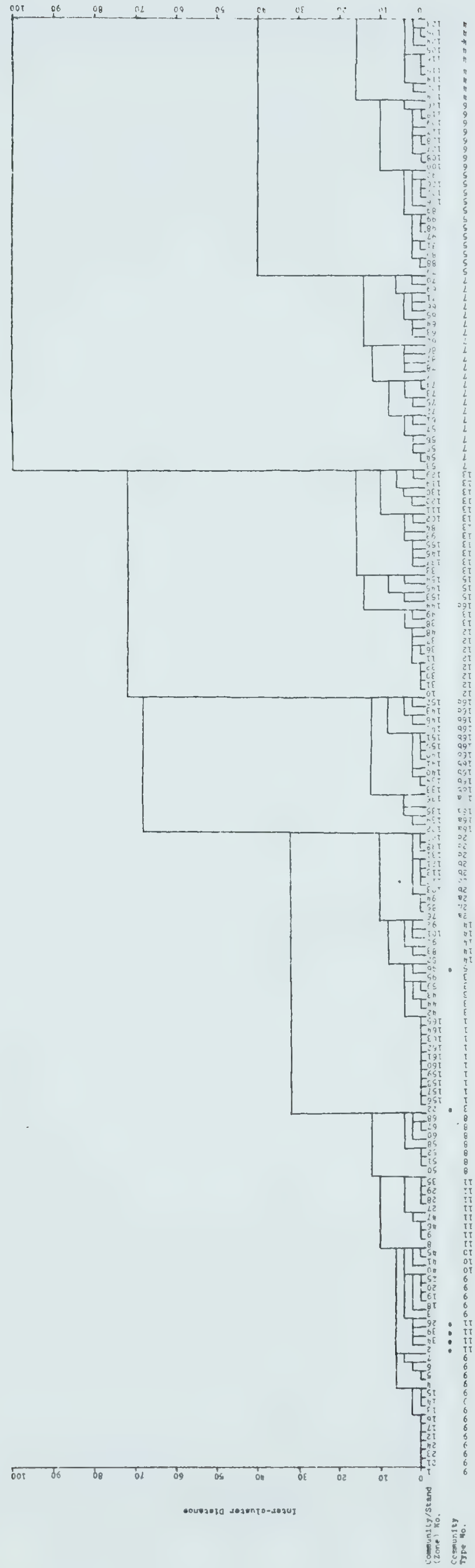
Each community was examined in relation to other communities in its cluster in the three techniques. The clusters among the three techniques were then compared and apparently misplaced communities noted. These communities

Figure 2. Cluster analysis: dengrogram for minimum variance technique of cluster formation (Pritchard & Anderson 1971) to determine community types (CT's) and subtypes (ST's) from 165 stands.

Legend:

1. Algal Aquatic CT
   Stands in the Revillon Coupé and the Lake Athabasca Marsh study areas (n=10). These totally dissimilar stands had no vascular plant species and were included in the analysis on the basis of the presence of algae.
2. *Utricularia vulgaris* (Vascular Aquatic) CT (n=10)
   a. *Glyceria striata* ST in the Chilaway Snye study area (n=3)
   b. *Lemna trisulca* ST in the Egg Lake study area (n=4)
   c. *Nuphar variegatum* ST in the Nuphar Lake study area (n=3)
3. *Equisetum fluviatile* (Herb Immature Marsh) CT (n=6)
4. *Carex atherodes* (Wet Meadow) CT (n=9)
5. *Salix petiolaris/Carex atherodes* (Meadow) CT (n=13)
6. *Salix bebbiana/S. bebbiana/Carex atherodes* (Fen) CT (n=8)
7. *Salix lutea/Carex atherodes* (Marsh) CT (n=22)
8. *Salix interior/Typha latifolia* (Shrub Immature Marsh) CT (n=7)
9. *Salix interior/Equisetum arvense* (Levee Herb) CT (n=19)
10. *Alnus tenuifolia/Epilobium angustifolium* (Swale Shrub) CT (n=3)
11. *Alnus tenuifolia/Cornus stolonifera* (Levee Shrub) CT (n=12)
12. *Populus balsamifera/Cornus stolonifera/Equisetum pratense* (Levee Tree) CT (n=8)
13. *Picea glauca/Rosa acicularis/Viburnum edule* (Upland Forest) CT (n=14)
14. *Salix bebbiana/S. bebbiana/Equisetum pratense* (Moist Lowland Forest) CT (n=5)
15. *Picea glauca/Alnus tenuifolia/Geocaulon lividum* (Wet Lowland Forest) CT (n=13)
16. *Myrica gale/M. gale* (Bog) CT (n=16)
   a. *Calla palustris* (Immature Hummock) ST (n=4)
   b. *Larix laricina/L. laricina/Ledum groenlandicum* (Mature Hummock) ST (n=9)
   c. *Alnus tenuifolia/Fragaria vesca* (Overmature Hummock) ST (n=3)

* Misplaced Stands


Inter-cluster Distance
Community/Stand (Zone) No.
Community Type No.

were re-examined and included in more appropriate clusters. Misplaced communities (2, 22, 26, 34, 38, 39, 49, 96, 144) are shown in Figure 2. Communities 2, 26, 34, and 39 were eventually put in cluster 11 because the other two techniques had placed them in this cluster. Similarly, community 144 was put in cluster 16 even though it had occurred in cluster 15. Community 22 was placed in cluster 3 because of its similar floristic composition even though all three techniques had put it with totally dissimilar communities in cluster 1. Communities 38 and 49 were associated with clusters 12 and 13, but were eventually put in the latter cluster because of their similar floristic compositions. Community 96 was associated with clusters 3 and 5 but was eventually placed in the latter cluster because of its similar floristic composition. A case may be made for including cluster 10 with cluster 9. However, its different physiognomy and floristic composition are sufficient for recognition as a distinct cluster.

D. Vegetation Description

The description of community types in the text follows the sequence shown in Table 1. The values given in the table are mean similarity values among community types based on presence-absence data using Sørensen's co-efficient of similarity (1948). The sequence of community types generally represents an increasing trend

Table 1. Matrix of similarity values(%) between community types recognized by cluster analysis in Figure 2, using Sørensen's co-efficient with presence-absence data.

Community Type		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Algal Aquatic	1		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vascular Aquatic	2	.		4.4	11.1	0.9	0.6	0.6	0.5	.	.	.	.	.	0.5	.	2.7
Herb Immature Marsh	3	.	4.4		10.1	11.2	8.9	12.5	19.5	4.6	11.6	2.1	0.6	1.6	6.9	2.7	3.1
Wet Meadow	4	.	11.1	10.1		42.0	36.6	27.1	8.5	9.0	6.6	2.6	0.8	1.6	12.9	4.1	7.5
Meadow	5	.	0.9	11.2	42.0		52.3	42.6	14.6	12.6	21.7	9.4	2.6	5.7	22.0	10.8	8.0
Fen	6	.	0.6	8.9	36.6	52.3		36.5	5.7	7.5	16.9	13.4	10.4	13.0	33.8	16.8	6.5
Marsh	7	.	0.6	12.5	27.1	42.6	36.5		35.8	27.2	31.5	23.6	6.4	7.5	18.7	11.8	7.1
Shrub Immature Marsh	8	.	0.5	19.5	8.5	14.6	5.7	35.8		34.8	27.9	21.7	1.3	0.7	2.8	2.7	6.0
Levee Herb	9	.	.	4.6	9.0	12.6	7.5	27.2	34.8		39.0	32.6	2.4	2.3	3.7	3.8	2.4
Swale Shrub	10	.	.	11.6	6.6	21.7	16.9	31.5	27.9	39.0		43.9	13.6	12.7	17.4	16.2	5.6
Levee Shrub	11	.	.	2.1	2.6	9.4	13.4	23.6	21.7	32.6	43.9		34.3	18.4	18.1	18.6	2.7
Levee Tree	12	.	.	0.6	0.8	2.6	10.4	6.4	1.3	2.4	13.6	34.3		37.7	22.3	30.9	2.2
Upland Forest	13	.	.	1.6	1.6	5.7	13.0	7.5	0.7	2.3	12.7	18.4	37.7		21.9	38.8	2.7
Moist Lowland Forest	14	.	0.5	6.9	12.9	22.0	33.8	18.7	2.8	3.7	17.4	18.1	22.3	21.9		25.7	4.7
Wet Lowland Forest	15	.	.	.2.7	4.1	10.8	16.8	11.8	2.7	3.8	16.2	18.6	30.9	38.8	25.7		13.6
Bog	16	.	2.7	3.1	7.5	8.0	6.5	7.1	6.0	2.4	5.6	2.7	2.2	2.7	4.7	13.6	
Mean similarity among communities within the community type.		.	58.1	31.4	57.7	63.2	65.6	55.1	54.1	50.7	63.5	53.2	59.5	53.7	37.8	54.3	54.2

toward improved soil drainage; greater soil development and environmental stability and amelioration; and greater community age, biotic structure, interaction and organization.

Species richness and percent cover for zonal attributes in 16 community types in the study region are given in Table 2.

The relationships of zones and community types to topography and height above MSWL are given in Figure 3.

Species abundance data in species/community tables and in Appendix 9 are Prominence Values:
$PV = \%\ \text{cover} \times \sqrt{\%\ \text{frequency}}$ (Stringer & La Roi 1970).
The mid-points of cover classes were used instead of % mean cover values to compensate for changing species covers during the growing season in the study region.

Distribution relationships of species among community types in the study region are shown in Appendix 9. The procedure used in preparing the table was based upon the principles given by Braun-Blanquet (1932), the manual methods outlined by Küchler (1967), and the computer programme developed by Češka and Roemer (1971).

Only three strata (Tree/Shrub/Herb-Dwarf Shrub) are recognized in naming community types. Development in these strata is described as follows: very poor (<21% stratal cover), poor (21-40%), moderate (41-60%),

Table 2. Averages and ranges[a] of percent cover for zonal attributes and species richness in 16 plant community types in the study region.

Zonal Attributes	Community Type[b,c]															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	10	*10*	*6*	*9*	*13*	*8*	*22*	*7*	*19*	*3*	*12*	*8*	*14*	*5*	*3*	*16*
Water	100	92	38	38	2	.	15	.	2	.	.	.	.	1	.	4
	0	*38-98*	*0-85*	*0-85*	*0-20*	.	*0-98*	.	*0-38*	.	.	.	.	*0-3*	.	*0-20*
Bare Ground	100	51[d]	90	26	8	3	41	96	96	4	30	0.1	+	.	.	1
	0	*3-85*	*85-98*	*0-68*	*0-38*	*0-10*	*0-98*	*85-98*	*85-98*	*0-10*	*0-85*	*0-+*	*0-3*	.	.	*0-3*
Detritus	.	0.3	5	69	76	91	21	2	3	89	50	87	82	78	58	20
	.	*0-3*	*+-20*	*20-98*	*38-98*	*68-98*	*+-85*	*+-3*	*0-10*	*85-98*	*3-98*	*85-98*	*68-85*	*68-85*	*38-68*	*10-38*
Woody Detritus	.	0.3	5	1	2	2	6	2	1	2	19	11	8	20	8	3
	.	*0-3*	*0-10*	*0-3*	*0-10*	*0-10*	*0-38*	*0-3*	*0-3*	*+-3*	*3-38*	*3-20*	*3-10*	*10-38*	*3-10*	*0-3*
Liverwort	.	.	.	0.1	.	.	0.3	0.1	.	1	0.3	.	.	.	.	.
	.	.	.	*0-+*	.	.	*0-+*	*0-+*	.	*0-3*	*0-3*	.	.	.	.	.
Mushroom	.	.	.	0.1	0.4	0.4	0.4	.	.	0.2	0.2	0.3	0.2	0.2	0.2	0.3
	.	.	.	*0-+*	*0-+*	*0-+*	*0-3*	.	.	*0-+*	*0-+*	*0-+*	*0-+*	*0-+*	*0-+*	*0-+*
Moss	.	.	0.2	5	19	8	33	0.4	0.4	4	3	2	8	8	42	76
	.	.	*0-+*	*+-20*	*0-38*	*+-38*	*0-68*	*0-3*	*0-3*	*+-10*	*0-10*	*+-3*	*+-38*	*3-20*	*20-68*	*68-85*
Lichen	.	.	.	.	.	0.4	.	.	.	0.2	0.1	0.3	1	1	0.5	0.6
	.	.	.	.	.	*0-3*	.	.	.	*0-+*	*0-+*	*0-+*	*+-3*	*+-3*	*0*	*0-3*
H-DS[e] Stratum	.	76	36	79	61	59	61	25	43	48	20	36	60	18	73	60
	.	*38-98*	*+-68*	*68-85*	*38-98*	*10-35*	*38-85*	*20-38*	*3-85*	*38-68*	*3-38*	*20-68*	*20-85*	*10-20*	*68-85*	*20-85*
No. of H-DS Species	.	7	9	21	19	21	31	15	10	15	11	8	23	12	30	23
	.	*5-9*	*2-13*	*13-28*	*14-26*	*15-27*	*20-46*	*10-24*	*2-20*	*11-18*	*4-18*	*5-10*	*14-32*	*9-17*	*26-34*	*16-36*
Shrub Stratum	.	.	.	10	27	37	34	20	27	53	78	68	63	40	68	68
	.	.	.	*0-68*	*0-68*	*10-85*	*3-68*	*3-38*	*3-68*	*38-85*	*10-98*	*38-98*	*10-85*	*10-68*	*0*	*38-98*
No. of Shrub Species	.	.	.	1	3	2	4	3	3	4	5	5	7	3	7	8
	.	.	.	*0-3*	*0-5*	*1-5*	*2-6*	*2-4*	*2-4*	*3-5*	*4-6*	*3-8*	*5-10*	*1-4*	*5-11*	*3-11*
Tree Stratum	.	.	.	2	0.04	31	1	.	.	12	23	89	78	56	89	9
	.	.	.	*0-20*	*0-+*	*0-85*	*0-20*	.	.	*0-38*	*0-85*	*68-98*	*38-85*	*38-85*	*85-98*	*0-38*
No. of Tree Species	.	.	.	0.1	0.1	0.6	0.1	.	.	0.3	0.5	3	4	2	5	0.8
	.	.	.	*0-1*	*0-1*	*0-1*	*0-1*	.	.	*0-1*	*0-3*	*2-4*	*1-5*	*1-4*	*4-6*	*1-2*
Total No. of Species	.	7	9	22	20	22	32	16	11	16	12	11	27	14	34	25
	.	*5-9*	*2-13*	*13-28*	*15-28*	*17-30*	*20-47*	*12-26*	*3-29*	*11-20*	*5-18*	*6-17*	*18-34*	*11-21*	*29-37*	*19-39*

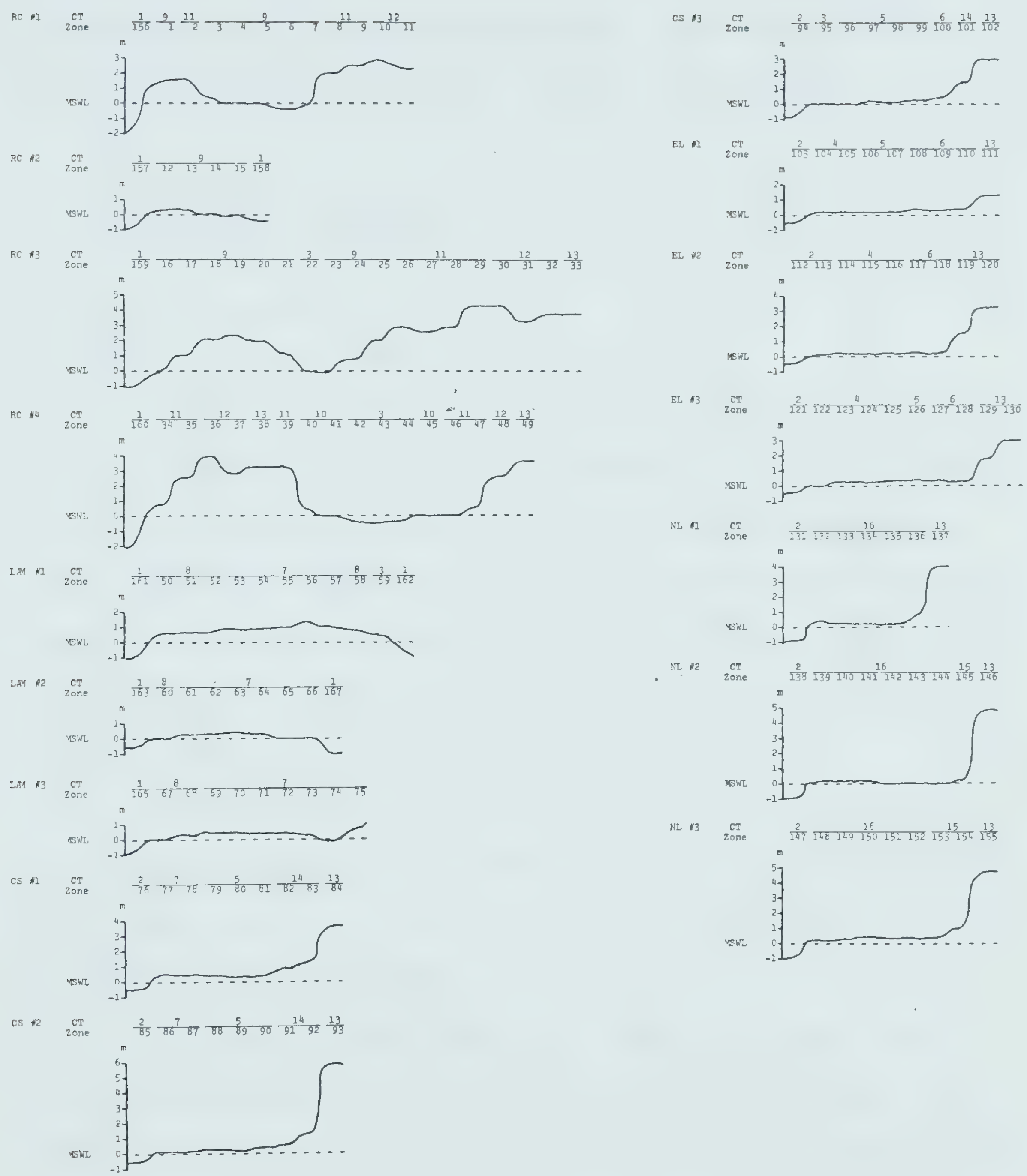
a Ranges given in italicized numbers.
b Names of community types given in Figure 2.
c Number of zones given in italicized numbers.
d Submerged vegetation cover in the Vascular Aquatic CT is 48% (range: 10-98%).
\+ Value of 0.5.
e Herb-Dwarf Shrub.

Figure 3. Diagrammatic representation of zones and community types at 16 study sites in relation to topography and height in metres (m) above mean summer water level (MSWL). The zones at each site are shown as being of equal length which causes highly variable vertical exaggeration in relief.

Legend:

RC: Revillon Coupé study area
LAM: Lake Athabasca Marsh study area
CS: Chilaway Snye study area
EL: Egg Lake study area
NL: Nuphar Lake study area
CT: Community Type

1. Algal Aquatic CT
2. *Utricularia vulgaris* (Vascular Aquatic) CT
3. *Equisetum fluviatile* (Herb Immature Marsh) CT
4. *Carex atherodes* (Wet Meadow) CT
5. *Salix petiolaris/Carex atherodes* (Meadow) CT
6. *Salix bebbiana/S. bebbiana/Carex atherodes* (Fen) CT
7. *Salix lutea/Carex atherodes* (Marsh) CT
8. *Salix interior/Typha latifolia* (Shrub Immature Marsh) CT
9. *Salix interior/Equisetum arvense* (Levee Herb) CT
10. *Alnus tenuifolia/Epilobium angustifolium* (Swale Shrub) CT
11. *Alnus tenuifolia/Cornus stolonifera* (Levee Shrub) CT
12. *Populus balsamifera/Cornus stolonifera/Equisetum pratense* (Levee Tree) CT
13. *Picea glauca/Rosa acicularis/Viburnum edule* (Upland Forest) CT
14. *Salix bebbiana/S. bebbiana/Equisetum pratense* (Moist Lowland Forest) CT
15. *Picea glauca/Alnus tenuifolia/Geocaulon lividum* (Wet Lowland Forest) CT
16. *Myrica gale/M. gale* (Bog) CT


RC #1
RC #2
RC #3
RC #4
LAM #1
LAM #2
LAM #3
CS #1
CS #2
CS #3
EL #1
EL #2
EL #3
NL #1
NL #2
NL #3
CT
Zone
m
MSWL

high (61-80%), and very high (>80%).

References to Appendices 2 and 3, after soil physical and chemical properties have been described in the environment section of the community type description, have been omitted to avoid needless repetition.

E. Description of Community Types (CT's) and Their Environments

1. Algal Aquatic CT
Zone # 156-165 (Fig. 2)

This CT is composed of 10 communities and is common in exposed locations of the lowest portions of channels in the RC and LAM study areas. This CT precedes Levee Herb and Levee Shrub CT's in the RC study area, and Herb Immature Marsh, Shrub Immature Marsh, and Marsh CT's in the LAM study area (Fig. 3). This type is totally dissimilar (100%) to all other CT's (Table 1).

There are no vascular species present in ths CT although non-rooted stem fragments of *Potamogeton pectinatus* were found in waters of the LAM study area. This CT is the youngest recorded.

In the RC study area, the range in water-level fluctuations was *ca.* 110 cm during the 1970 growing season and 190 cm in 1971. The greatest water-level fluctuations occur during and just after spring floods. The Coupé

channel has extremely variable flow rates, water depths averaging 6 m, high and variable suspended loads, high erosive and abrasive waters, and highly unstable substrates. Ice scouring during spring floods is quite severe and has a pronounced effect on channel sides. Wave action and reversing current regime throughout the growing season contribute to the constantly changing aquatic environment of the study area.

In the LAM study area, the range in water-level fluctuations was *ca.* 115 and 175 cm during the summers of 1970 and 1971. Channels in this area differ from the Coupé by having deeper water averaging 9 m, higher fine-textured suspended load, higher sedimentation rate, less erosive and abrasive waters, and a relatively more stable substrate. The above factors have effectively eliminated all hydrophytic vascular species from the RC and LAM study areas.

Vegetational and environmental characteristics suggest that this CT is an unstable stage controlled by allogenic factors. This highly distinct and quite variable CT is comparable to the Water Habitat Type of Townsend (1973b) and the Flowing Stream and River CT of the Water Channel Landscape Type of Dirschl *et al.* (1974).

2. *Utricularia vulgaris* (Vascular Aquatic) CT
Zone # 76, 85, 94, 103, 112, 113, 121, 131, 138, 147 (Fig. 2)

a. Vegetation

This CT is composed of 10 communities and is common in generally exposed locations of the lowest portions of the CS, EL, and NL basins. This CT precedes Marsh, Herb Immature Marsh, Wet Meadow, and Bog CT's (Fig. 3). This type is most similar to the Wet Meadow CT. Mean similarity among its communities is 58% (Table 1).

This CT has three subtypes. The *Glyceria striata* ST is composed of three communities (76, 85, 94: Table 3) representing the last stage in the open, surface drainage status. This ST is restricted to the CS study area and has moderately low similarities to the second (50%) and third (43%) ST's. It is comparable to the Shallow and Open, Freely Drained CT of the Standing Water Landscape Type of Dirschl *et al.* (1974).

The *Lemna trisulca* ST is composed of four communities (103, 112, 113, 121: Table 3) having a restricted surface drainage status. This ST is exclusive to the EL study area and has a moderately low similarity to the third (51%) ST. It is comparable to the Open, Restricted Drainage CT of the Standing Water Landscape Type of Dirschl *et al.* (1974).

Table 3. Species prominence in the *Utricularia vulgaris* (Vascular Aquatic) Community Type.

Study Area		Chilaway Snye			Egg Lake				Nuphar Lake			$\bar{x}$
Site Number		3	2	1	1	2	2	3	1	2	3	
Zone Number		94	85	76	103	112	113	121	131	138	147	
Subtype		A	A	A	B	B	B	B	C	C	C	
Species Composition												
Herb-Dwarf Shrub Stratum: D		9	8	8	8	9	8	5	7	5	5	7.2
Utricularia vulgaris	+	375[a]	45	19	850	675	658	850	375	675	375	490
Nuphar variegatum	*	.	.	.	.	.	.	.	126	290	604	102
Potamogeton richardsonii	*	126	179	179	78	179	.	.	.	.	.	74
P. zosteriformis	*	2	13	2	78	179	19	.	89	179	63	62
Glyceria striata	+	3	155	168	.	.	.	.	.	.	.	33
Myriophyllum exalbescens	+	2	2	2	2	2	2	2	290	2	3	31
Lemna minor	+	.	.	.	100	2	23	89	2	.	.	22
L. trisulca		.	.	.	2	100	3	63	.	.	.	17
Sparganium minimum	+	.	.	.	.	.	.	.	19	3	89	11
Carex atherodes		.	.	.	.	.	78	.	.	.	.	7.8
Sagittaria cuneata	+	2	2	19	.	.	19	.	.	.	.	4.2
Ceratophyllum demersum		.	.	.	2	2	2	2	27	.	.	3.5
Potamogeton gramineus	*	2	19	3	.	.	.	.	.	.	.	2.4
Sparganium angustifolium		.	.	.	.	19	.	.	.	.	.	1.9
Alisma plantago-aquatica	+	2	2	2	2	2	.	.	.	.	.	1.0
Potamogeton pusillus	*	2	.	.	.	.	.	.	.	.	.	0.2

$\bar{x}$ *Mean.*
A *Glyceria striata* Subtype.
B *Lemna trisulca* Subtype.
C *Nuphar variegatum* Subtype.
D Number of species.
a Prominence value (rounded off).
\+ Species achieving their highest prominence values in this community type.
* Species exclusive to this community type.

The *Nuphar variegatum* ST is composed of three communities (131, 138, 147: Table 3) having an isolated surface drainage status. This ST is exclusive to the NL study area. It is comparable to the Open, Severely Restricted Drainage CT of the Standing Water Landscape Type of Dirschl *et al.* (1974).

The mean number of vascular species per community is 7, the 2nd lowest recorded (Table 2). Five herb species are exclusive to this CT and seven have their highest mean PV's here (Table 3, App. 9). This CT has a highly developed herb-dwarf shrub stratum (Pl. 6), the 2nd lowest detritus and woody detritus covers, with bryophytes, mushrooms, and lichens being absent. This CT has no live shrub and tree species although sparsely scattered dead clumps of *Salix* spp., which are not present in the quadrats, do occur in the EL study area (Table 2). Total biomass averages 1,000 kg/ha with forbs contributing all the weight (Table 4). Representative age is 1-3 years, the 2nd youngest CT.

Herb-Dwarf Shrub Stratum

This stratum is composed of 12 forbs and 4 graminoids with dwarf shrubs being totally absent (Table 3). Average cover of this stratum is 76%, the 2nd highest recorded (Table 2). *Utricularia vulgaris* is the most

Plate 6. *Nuphar variegatum* community in the *Utricularia vulgaris* (Vascular Aquatic) Community Type adjacent to site #2 in the Nuphar Lake study area.

Table 4. Average oven-dry understory biomass[a] (kg/ha) for above-ground plant growth-form groups in 13 community types in the study region.

Community Type[b]	Growth-form Group					
	Bryoids	Graminoids	Forbs	Dwarf Shrubs	Shrubs	Total
Algal Aquatic (3)[c]	.	.	.	.	.	.
Vascular Aquatic (3)	.	.	997.0	.	.	997.0
Wet Meadow (3)	0.7	6540.0	8.7	.	.	6549.4
Meadow (3)	3.3	2280.0	48.0	311.3	167.7	2810.3
Fen (2)	.	2729.0	18.0	.	.	2747.0
Marsh (7)	16.9	291.6	64.7	54.4	261.6	689.2
Shrub Immature Marsh (4)	5.0	173.0	62.0	43.2	108.0	391.2
Levee Herb (5)	1.0	4.5	305.7	86.2	341.7	739.1
Levee Shrub (3)	10.0	0.3	48.3	94.0	1172.0	1324.6
Levee Tree (2)	10.5	.	145.5	27.5	205.0	388.5
Upland Forest (5)	36.0	42.2	291.6	78.8	443.8	892.4
Moist Lowland Forest (2)	1.0	401.5	5.0	0.5	432.0	840.0
Bog (5)	995.6	1243.0	641.0	244.2	252.0	3375.8

a Sampling conducted during the last week in June and first week in July 1971.

b No sampling in Herb Immature Marsh, Swale Shrub, and Wet Lowland Forest Community Types.

c Number of samples.

prominent species followed, to a much lesser extent, by *Nuphar variegatum*. The remaining species have low PV's and are relatively unimportant in this CT. *Nuphar variegatum*, *Potamogeton richardsonii*, *P. zosteriformis*, *P. gramineus*, and *P. pusillus* are exclusive to this CT (Table 3, App. 9).

b. Environment

In the CS study area, the range of water-level fluctuations was *ca.* 250 cm during the summer of 1971. However, water-level fluctuations here are generally less severe than those in the RC and LAM areas of the preceding CT. Negligible current velocity, decreased water depth averaging slightly over 100 cm, more stable substrates, and greater accumulation of fine-textured sediments occur in channels draining the area.

In the EL study area, the range of water-level fluctuations was *ca.* 21 and 25 cm during the summers of 1970 and 1971, *i.e.* much less than in the previous three study areas and mostly accountable to drawdown by evapotranspiration. The higher river water levels in 1971 had no access to Egg Lake and thus its drawdown continued unimpeded. However, the area was flooded but not ice-scoured in the spring of 1972 after ice-jamming on the Peace River. The 1972 water level was *ca.* 75 cm higher than in 1971 when the lake had a maximum water depth of

only *ca*. 100 cm and high water clarity. Wave action was not intense during the study period.

In the NL study area, the range of water-level fluctuations was *ca*. 8 and 7 cm during the summers of 1970 and 1971, by far the narrowest of the five study areas. In contrast with EL, this study area was not flooded in 1972 and its water levels that year were not noticeably different from those of 1970 and 1971. Although remnants of the old channel connection to the Coupé are in places as much as 4 m deep, the lake portion of the basin averages about 150-180 cm in depth. The "false" lake bottom (*i.e.*, surface of spongy organic matter) is relatively flat to within 10 m of the shoreline. This area is rarely if ever flooded now as indicated by the presence of an organic lake bottom surrounded by extensive Precambrian outcrops and well-developed levees.

c. Integration

This CT occupies the hydric segment of the moisture gradient. ***Utricularia vulgaris, Glyceria striata, Myriophyllum exalbescens,*** and four other species achieve their highest mean PV's here (Table 3, App. 9). These species and those exclusive to this CT are categorized as "hydrophytic".

Effects of water-level fluctuations, water chemistry, sedimentation, and erosion on the aquatic vegetation

have been reported, in detail, previously by Doherty and La Roi (1973) and briefly described in the "Deltaic Environment" section of this thesis. The above factors have an important bearing on the distribution of aquatic species in all study areas.

Vegetational and environmental characteristics suggest that the *Glyceria striata* ST is a relatively unstable stage controlled by allogenic factors, the *Lemna triculca* ST is a relatively stable stage controlled by polygenic factors, and the *Nuphar variegatum* ST is a stable stage controlled by autogenic factors. Seral sequences in the EL study area were previously initiated by allogenic factors but presently are controlled by polygenic factors. This highly distinct but variable CT is comparable to the Aquatic Association of Raup (1935), the Emergent Habitat Type of Townsend (1973b), and CT's of the Standing Water Landscape Type of Dirschl *et al.* (1974).

3. *Equisetum fluviatile* (Herb Immature Marsh) CT
Zone # 22, 42-44, 59, 95 (Fig. 2)

a. Vegetation

This CT is composed of six communities. Community 22 is located between those of the Levee Herb CT and 42-44 are located between those of the Swale Shrub CT in the RC study area, while 59 and 95 occur between those of the Algal Aquatic and Shrub Immature Marsh and between those

of the Vascular Aquatic and Meadow CT's in the LAM and CS study areas respectively (Fig. 3). This CT generally occurs in sheltered locations and is of limited extent in these study areas (Fig. 3). It is most similar to the Shrub Immature Marsh CT. Mean similarity among its communities is only 31%, the 2nd lowest recorded (Table 1). No subtypes are recognized in this CT (Table 5).

The mean number of vascular species per community is 9, the 3rd lowest recorded (Table 2). Two herb species are exclusive to this CT and four have their highest mean PV's in it (Table 5, App. 9). This CT has a poorly developed herb-dwarf shrub stratum (Pl. 7), and the 3rd lowest moss cover, with liverworts, mushrooms, lichens, shrubs, and trees being absent (Table 2). No biomass sampling was conducted in this CT (Table 4). Representative age is only 3 years, the same as in the preceding CT.

Herb-Dwarf Shrub Stratum

This stratum is composed of 18 forbs, 12 graminoids, and 1 horsetail with dwarf shrubs being totally absent (Table 5). Its average cover is 36% (Table 2). *Equisetum fluviatile* is most dominant, followed by *Typha latifolia* and, to a much lesser extent, by *Carex atherodes*, *Scirpus validus*, *Glyceria striata*, *Eleocharis palustris*, and *Rorippa islandica*. *Scirpus microcarpus* and *Utricularia intermedia* are the only species exclusive to this CT (Table 5, App. 9).

Table 5. Species prominence in the *Equisetum fluviatile* (Herb Immature Marsh) Community Type.

Study Area	RC			LAM	CS	RC	$\bar{x}$
Site Number	4	4	4	1	3	3	
Zone Number	42	44	43	59	95	22	
Species Composition							
Herb-Dwarf Shrub Stratum: A	10	13	9	6	12	2	8.7
Equisetum fluviatile +	200[a]	375	200	2	.	.	130
Typha latifolia +	78	63	200	155	3	2	84
Carex atherodes	63	63	63	2	78	.	45
Scirpus validus +	.	.	.	126	126	.	42
Glyceria striata	.	.	.	.	179	.	30
Eleocharis palustris	.	.	.	.	100	2	17
Rorippa islandica	.	63	.	.	.	.	10
Sparganium angustifolium +	.	.	2	23	3	.	4.7
Calamagrostis canadensis	.	.	.	.	19	.	3.2
Eleocharis acicularis	.	.	.	.	19	.	3.2
Carex bebbii	2	2	2	.	.	.	1.0
Arenaria lateriflora	2	2	.	.	.	.	0.7
Potentilla norvegica	2	2	.	.	.	.	0.7
Senecio congestus	.	2	2	.	.	.	0.7
Lysimachia thyrsiflora	.	3	.	.	.	.	0.5
Plantago major	.	3	.	.	.	.	0.5
Sagittaria cuneata	.	.	.	.	3	.	0.5
Rumex maritimus	2	.	.	.	.	.	0.3
Stellaria longifolia	2	.	.	.	.	.	0.3
Ranunculus cymbalaria	2	.	.	.	.	.	0.3
Artemisia biennis	2	.	.	.	.	.	0.3
Parnassia palustris	.	2	.	.	.	.	0.3
Potentilla anserina	.	2	.	.	.	.	0.3
Epilobium angustifolium	.	2	.	.	.	.	0.3
Alopecurus aequalis	.	.	2	.	.	.	0.3
Scirpus microcarpus *	.	.	2	.	.	.	0.3
Utricularia intermedia *	.	.	2	.	.	.	0.3
Carex sychnocephala	.	.	.	2	.	.	0.3
Juncus balticus	.	.	.	.	2	.	0.3
Limosella aquatica	.	.	.	.	2	.	0.3
Utricularia vulgaris	.	.	.	.	2	.	0.3

RC Revillon Coupé study area.
LAM Lake Athabasca Marsh study area.
CS Chilaway Snye study area.
$\bar{x}$ Mean.
A Number of species.
a Prominence value (rounded off).
\+ Species achieving their highest prominence values in this community type.
* Species exclusive to this community type.

Plate 7. *Equisetum fluviatile* community in the *E. fluviatile* (Herb Immature Marsh) Community Type of zone 44 at site #4 in the Revillon Coupé study area.

b. Environment

Zone 22 occurs in a very exposed swale at site #3; zones 42-44 occur in a sheltered swale in a point-bar channel behind a log-jam at one end and a levee at the other end, at site #4 in the RC study area; and zones 59 and 95 are located on channel banks in the LAM and CS study areas respectively. The very flood prone zones have an average height of 0.1 m ASWL (range: 0-0.4 m) and are very frequently flooded for up to four months during the growing season.

The poorly developed and neutral (7.2) to mildly alkaline (7.6) soils of this CT are Regosols. The soils have high conductivity, sulphate, and available nitrogen values; medium sodium, calcium carbonate, and available potassium values; and low available phosphorus values. Sedimentation rates are moderate to high. Textural classes are mostly sandy loam, followed by loam and sandy clay loam. Sand content is the most variable and is the dominant fraction (57%). The average sand:clay (S:C) ratio is 5.0, the 4th highest recorded (range: 1.9-9.6). The average organic matter content is low. The topography ranges from depressional to gently sloping zones. The mean field soil moisture content is 39% (31-67%). These values are slightly more than field capacity (FC) and *ca.* 4x the permanent wilting point (PWP), indicating a moderate (moderate refers to field soil moisture contents around FC and 2-4x PWP) soil moisture surplus from the influence of the

hydrologic regime. This conclusion is substantiated by soil moisture samples taken during the growing season. The small variations in the soil moisture regime reflect uniformity in zonal conditions, e.g. soil texture. Mostly imperfectly drained and, to a much smaller extent, poorly drained conditions exist in this CT.

c. Integration

This CT occupies the hydric to mesic range of the moisture gradient. *Equisetum fluviatile*, *Typha latifolia*, and two other species have their highest mean PV's here (Table 5, App. 9). These species and those exclusive to this CT are categorized as "subhydrophytic".

This CT occurs only where there is sufficient protection from water-level fluctuations to permit conditions favourable for marsh initiation. For example, the swale communities 42-44 located behind the log-jam are annually flooded but then have fairly stable above-ground water levels. *Equisetum fluviatile* and *Typha latifolia* prefer inorganic substrates and relatively stable water levels that experience a net drawdown during the growing season. These species appear to tolerate only limited annual alluviation by coarse-textured sediment. Harris and Marshall (1963) have shown that *T. latifolia* will have reduced abundance and vitality if the water depth is over 30 cm in the third year of reflooding, and die out completely if these water levels are maintained into the fourth year.

They have also shown that *Scirpus validus* will die out in the second year of reflooding if the water depth is over 38 cm. These constraints occur in other CT's but not in this CT. These and other species exhibit excellent vitality in this CT. Any change from stable but declining water levels, and uniform sedimentation types and rates may drastically alter communities in this CT.

Vegetational and environmental characteristics suggest that this CT is an unstable stage controlled by allogenic factors. This highly distinct CT is comparable to the Herbaceous and Shore Associations of Raup (1935), the Emergent Habitat Type of Townsend (1973b), and the Immature Fen CT of Dirschl *et al.* (1974).

4. *Carex atherodes* (Wet Meadow) CT
Zone # 104, 105, 114-116, 122-125 (Fig. 2)

a. Vegetation

This CT is composed of 9 communities located in generally exposed areas between Vascular Aquatic and Meadow or Fen CT's. It is common only in the EL study area (Fig. 3). It is most similar to the Meadow, followed by Fen and Marsh CT's. Mean similarity among its communities is 58% (Table 1). There are no subtypes in this CT (Table 6).

The mean number of vascular species per community is 22 (Table 2). Four herb species are exclusive to this CT, and 15 species in the herb-dwarf shrub stratum have

Table 6. Species prominence in the *Carex atherodes* (Wet Meadow) Community Type.

Study Area		Egg Lake									$\bar{x}$
Site Number		1	3	3	3	3	1	2	2	2	
Zone Number		104	122	123	124	125	105	116	115	114	
Species Composition											
Tree Stratum: A		.	.	.	.	.	.	1	.	.	0.1
Salix bebbiana		.	.	.	.	.	.	89[a]	.	.	9.9
Shrub Stratum: A		.	.	.	2	1	.	3	1	.	0.8
Salix petiolaris		.	.	.	3	2	.	168	89	.	29
S. pyrifolia		.	.	.	.	.	.	168	.	.	19
S. serissima		.	.	.	.	.	.	89	.	.	9.9
S. pseudomonticola		.	.	.	2	.	.	.	.	.	0.2
Herb-Dwarf Shrub Stratum: A		27	22	28	23	18	23	18	18	13	21
Carex atherodes		100	30	200	375	375	375	675	375	850	373
Scolochloa festucacea	+	89	4	23	2	155	78	23	375	78	92
Rorippa islandica	+	78	200	100	3	3	200	2	2	2	66
Bidens cernua	+	19	63	200	2	2	89	3	89	3	52
Glyceria grandis	+	.	4	4	375	.	.	.	.	.	43
Rumex maritimus	+	3	89	200	2	.	63	.	.	.	40
Ranunculus macounii	+	.	30	27	78	100	89	19	2	.	38
Lemna trisulca	+	237	.	.	.	.	.	.	100	2	38
Utricularia vulgaris		179	126	.	.	.	.	.	23	2	37
Carex sychnocephala	+	3	23	200	.	.	27	.	.	.	28
Calamagrostis canadensis		63	.	.	2	2	179	2	.	.	28
Lemna minor		2	19	.	.	.	.	27	100	27	19
Scutellaria galericulata		.	.	115	2	3	2	.	.	.	18
Galium trifidum		.	2	2	3	89	27	30	2	3	18
Ranunculus pensylvanicus	+	63	.	3	78	2	2	.	.	.	16
Salix petiolaris	+	.	.	2	63	23	2	19	3	23	15
Ranunculus natans	+	23	.	.	23	2	30	27	3	27	15
Polygonum amphibium		30	.	2	2	2	89	2	2	.	14
Myriophyllum exalbescens		3	.	.	.	.	.	3	100	2	12
Epilobium glandulosum		.	3	23	30	27	3	2	2	3	10
Erigeron philadelphicus		.	.	.	.	.	.	78	5	.	9.2
Ranunculus sceleratus	+	4	2	3	27	.	3	27	2	2	7.8
Typha latifolia		.	.	63	.	.	.	.	.	.	7.0
Stellaria crassifolia		.	.	19	4	2	19	2	2	.	5.3
Salix pyrifolia		.	.	27	2	19	.	.	.	.	5.3
Ceratophyllum demersum	+	45	.	.	.	.	.	.	.	.	5.0
Juncus bufonius	+	3	4	3	23	.	.	.	.	.	3.7
Stachys palustris		.	2	2	2	2	.	19	2	.	3.2
Acorus calamus	*	27	.	.	.	.	.	.	.	.	3.0
Sium suave		.	2	.	.	3	2	19	.	.	2.9
Sparganium angustifolium		23	.	.	.	.	3	.	.	.	2.9
Beckmannia syzigachne		2	.	23	.	.	.	.	.	.	2.8
Ranunculus aquatilis	*	23	2	.	.	.	.	.	.	.	2.8
R. pedatifidus	*	2	2	2	.	.	2	.	.	.	0.9
Sonchus arvensis	*	.	.	4	2	.	2	.	.	.	0.9
Carex rostrata		2	2	2	.	.	.	.	.	.	0.7
Mentha arvensis		.	.	2	2	2	.	.	.	.	0.7
Alopecurus aequalis	+	2	2	.	.	.	.	.	.	.	0.4
Deschampsia caespitosa		2	2	.	.	.	.	.	.	.	0.4
Ranunculus gmelinii		2	2	.	.	.	.	.	.	.	0.4
Carex aquatilis		.	.	2	.	.	2	.	.	.	0.4
Alisma plantago-aquatica		3	.	.	.	.	.	.	.	.	0.3
Scirpus validus		.	.	3	.	.	.	.	.	.	0.3
Cicuta douglasii		.	.	2	.	.	.	.	.	.	0.2
Juncus balticus		.	.	.	2	.	.	.	.	.	0.2
Poa palustris		.	.	.	.	.	2	.	.	.	0.2

$\bar{x}$ Mean.
A Number of species.
[a] Prominence value (rounded off).
+ Species achieving their highest prominence values by stratum in this community type.
* Species by stratum exclusive to this community type.

their highest mean PV's here (Table 6, App. 9). This CT has very poorly developed tree and shrub strata and a highly developed herb-dwarf shrub stratum (Pl. 8). This CT has the 3rd lowest woody detritus cover, with lichens being absent (Table 2). Total understory biomass averages 6,500 kg/ha, the highest recorded, with graminoids contributing 99% (Table 4). Representative age of this CT is 18 years.

Tree Stratum

Average tree cover is only 2%. The mean number of species per community in this stratum is 0.1 (Table 2). ***Salix bebbiana*** is the sole species, and has a very low prominence and only attains sapling size here (Table 6). Total live and dead sapling densities are 9 and 200 stems/ha (Table 7); average heights of live and dead individuals are 5.1 and 7.0 m (Table 8). Dead willows are thus taller and more numerous than live ones here; true of no other CT. Average age at death is 18 years (Table 9). The tree stratum, therefore, does not appear to be a viable and contributing component of this CT.

Shrub Stratum

Average shrub cover is 10%, the 4th lowest recorded. The mean number of species per community in this stratum is 1, the 4th lowest recorded (Table 2). ***Salix***

Plate 8. *Rorippa islandica* community in the *Carex atherodes* (Wet Meadow) Community Type of zone 122 at site #3 in the Egg Lake study area.

Table 7. Average density (stems/ha) of live and dead[a] saplings[b], tallied by species in each community type in the study region.

Species	Community Type[c]										
	4	5	6	7	10	11	12	13	14	15	16
Larix laricina	.	.	.	.	.	.	.	.	.	.	35
	.	.	.	.	.	.	.	.	.	.	*115*
Picea glauca	.	.	.	.	.	.	30	474	.	773	5
	.	.	.	.	.	.	.	*29*	.	*107*	.
P. mariana	.	.	.	.	.	.	.	.	.	.	60
	.	.	.	.	.	.	.	.	.	.	*20*
Populus balsamifera	.	.	.	.	.	33	120	128	.	80	.
	.	.	.	.	.	*7*	*80*	*154*	*16*	*107*	.
P. tremuloides	.	.	.	.	.	.	.	560	368	27	.
	.	.	.	.	.	.	.	*251*	*16*	.	.
Salix arbusculoides	.	6	.	.	.	.	.	51	240	587	190
	.	.	.	.	.	.	.	*80*	*176*	*240*	*15*
S. bebbiana	9	.	4080	22	.	220	20	440	4880	.	.
	196	.	*790*	.	.	*167*	*30*	*489*	*608*	.	.
S. interior	.	.	.	.	1200	.	.	.	.	.	.
	.	.	.	.	*747*	.	.	.	.	.	.
S. scouleriana	.	.	.	.	.	.	.	.	112	.	.
	.	.	.	.	.	.	.	*40*	*112*	.	.
Alnus tenuifolia	.	.	.	.	.	200	1130	120	.	720	.
	.	.	.	.	.	*160*	*520*	*11*	.	*507*	*35*
Betula papyrifera	.	.	.	.	.	.	10	269	.	.	.
	.	.	.	.	.	.	.	*86*	.	*53*	.
Total	9	6	4080	22	1200	453	1310	2042	5600	2187	290
	196	.	*790*	.	*747*	*334*	*630*	*1140*	*928*	*1014*	*185*

[a] Dead density given in italicized numbers.
[b] Saplings include stems of the 3 to 8 cm dbh class.
[c] Names of community types given in Figure 2; CT's 1-3, 8, 9 have no saplings.

Table 8. Average height (m) of live and dead[a] saplings[b], tallied by species in each community type in the study region.

Species	Community Type[c] 4	5	6	7	10	11	12	13	14	15	16
Larix laricina	.	.	.	.	.	.	.	.	.	.	4.4
	.	.	.	.	.	.	.	.	.	.	*4.1*
Picea glauca	.	.	.	.	.	.	5.2	5.4	.	7.6	7.6
	.	.	.	.	.	.	.	*6.8*	.	*6.7*	.
P. mariana	.	.	.	.	.	.	.	.	.	.	5.0
	.	.	.	.	.	.	.	.	.	.	*3.7*
Populus balsamifera	.	.	.	.	.	7.2	4.5	6.4	.	9.0	.
	.	.	.	.	.	*6.7*	*4.2*	*4.6*	*6.5*	*6.8*	.
P. tremuloides	.	.	.	.	.	.	.	7.4	6.8	7.0	.
	.	.	.	.	.	.	.	*5.2*	*5.5*	.	.
Salix arbusculoides	.	4.2	.	.	.	.	.	6.9	4.2	4.1	3.9
	.	.	.	.	.	.	.	*4.7*	*3.9*	*3.4*	*3.7*
S. bebbiana	5.1	.	5.2	2.9	.	6.1	6.2	6.1	5.6	.	.
	7.0	.	*4.1*	.	.	*6.0*	*5.2*	*4.9*	*4.4*	.	.
S. interior	.	.	.	.	6.8	.	.	.	.	.	.
	.	.	.	.	*5.5*	.	.	.	.	.	.
S. scouleriana	.	.	.	.	.	.	.	.	5.5	.	.
	.	.	.	.	.	.	.	*3.8*	*4.9*	.	.
Alnus tenuifolia	.	.	.	.	.	7.0	6.2	5.7	.	4.9	.
	.	.	.	.	.	*5.3*	*4.8*	*3.8*	.	*4.8*	*2.2*
Betula papyrifera	.	.	.	.	.	.	5.2	5.2	.	.	.
	.	.	.	.	.	.	.	*4.9*	.	*3.6*	.
Average	5.1	4.2	5.2	2.9	6.8	6.8	5.5	6.2	5.5	6.5	5.2
	7.0	.	*4.1*	.	*5.5*	*6.0*	*4.7*	*4.8*	*5.0*	*5.1*	*3.4*

a Dead individuals given in italicized numbers.
b Saplings include stema of the 3 to 8 cm dbh class.
c Names of community types given in Figure 2; CT's 1-3, 8, 9 have no saplings.

Table 9. Average age (yrs) of saplings[a], tallied by species in each community type in the study region.

Species	Community Type[b]										
	4	5	6	7	10	11	12	13	14	15	16
Larix laricina	.	.	.	.	.	.	.	.	.	.	41
Picea glauca	.	.	.	.	.	.	21	28	.	21	--
P. mariana	.	.	.	.	.	.	.	.	.	.	43[c]
Populus balsamifera	.	.	.	.	.	25	34	49	--	--	.
P. tremuloides	.	.	.	.	.	.	.	40	--	--	.
Salix arbusculoides	.	--[e]	.	.	.	.	.	47	37[c]	--	--
S. bebbiana	18[c,d]	.	27	21[d]	.	34	27	52	25	.	.
S. interior	.	.	.	.	27[d]	.	.	.	.	.	.
S. scouleriana	.	.	.	.	.	.	.	40[c]	20	.	.
Alnus tenuifolia	.	.	.	.	.	35	30	--	.	19	10[c]
Betula papyrifera	.	.	.	.	.	.	--	41	.	--	.
Average age (live)	18[c]	--	27	21	27	31	28	43	22	20	41

a Saplings include stems of the 3 to 8 cm dbh class.
b Name of community types given in Figure 2; CT's 1-3, 8, 9 have no saplings.
c Dead individuals.
d Representative age: mean of the oldest species in the community type.
e Missing data.

petiolaris is the most prominent species. The other three species, *Salix pyrifolia*, *S. serissima*, and *S. pseudomon ticola*, are less abundant (Table 6). Total live and dead shrub densities are 2,730 and 2,670 stems/ha, with the former being the 4th lowest recorded. *Salix pyrifolia* and *S. petiolaris* contribute most to the live and dead densities, respectively (Table 10). This stratum has an average height of 22 dm (Table 11), and an average live age of 16 years (Table 12). The shrub stratum is a more viable component of this CT than the tree stratum, because its species seem more tolerant of periodic flooding.

Herb-Dwarf Shrub Stratum

This stratum is composed of 28 forbs, 16 graminoids, and 2 woody species (Table 6). The mean number of species per community in this stratum is 21, the 5th highest recorded. Average cover of this stratum is 79%, the highest recorded (Table 2). *Carex atherodes* is dominant, followed by *Scolochloa festucacea*, *Rorippa islandica*, and *Bidens cernua*. The other 42 species have much lower PV's and are relatively unimportant. Seven *Ranunculus* spp. occur here. *Acorus calamus*, *Ranunculus aquatilis*, *R. pedatifidus*, and *Sonchus arvensis* are exclusive to this CT (Table 6, App. 9). Total live dwarf-shrub density is 4,200 stems/ha (4th lowest recorded) with *S. petiolaris* the major contributor (Table 13).

Table 10. Average density(stems/ha) of live and dead[a] shrubs[b], tallied by species in each community type in the study region.

Species	Community Type[c] 4	5	6	7	8	9	10	11	12	13	14	15	16
Larix laricina	.	.	.	.	.	.	.	.	.	.	.	.	1530
	.	.	.	.	.	.	.	.	.	.	.	.	*1530*
Picea glauca	.	.	.	20	.	.	.	.	.	640	100	3670	.
	.	.	.	.	.	.	.	.	.	*70*	*100*	*2000*	*60*
P. mariana	.	.	.	.	.	.	.	.	.	.	.	.	810
	.	.	.	.	.	.	.	.	.	.	.	.	*190*
Populus balsamifera	.	.	.	460	430	.	.	2120	3620	390	.	170	.
	.	.	.	.	.	.	.	*80*	*310*	*70*	.	.	.
P. tremuloides	.	40	.	390	.	.	.	.	.	320	1700	.	.
	.	.	.	.	.	.	.	.	.	*360*	*700*	.	.
Salix arbusculoides	.	650	.	.	.	.	.	.	.	110	2700	2500	.
	.	.	.	.	.	.	.	.	.	.	*1400*	*3170*	.
S. barklayi (?)	.	.	.	.	.	.	.	.	.	.	.	500	500
	.	.	.	.	.	.	.	.	.	.	.	*170*	*500*
S. bebbiana	.	.	15600	8610	.	320	.	5460	560	610	7300	12200	160
	.	.	*7560*	*40*	.	.	.	*460*	.	*430*	*2600*	*8330*	*160*
S. glauca	.	.	60	.	.	.	.	.	.	.	.	170	30
	.	.	.	.	.	.	.	.	.	.	.	.	.
S. interior	.	.	.	28400	67600	13000	22000	14700	.	.	.	.	.
	.	.	.	*820*	.	*30*	*3670*	*420*	.	.	.	.	.
S. lasiandra	.	120	.	.	290	260	.	420	.	.	.	.	.
	.	*80*	.	.	.	.	.	*80*	.	.	.	.	.
S. lutea	.	9650	.	13800	11700	6050	4670	8960	.	.	.	.	.
	.	.	.	*20*	.	.	.	*210*	.	.	.	.	.
S. myrtillifolia	.	.	.	.	.	.	.	.	.	.	.	1330	4190
	.	.	.	.	.	.	.	.	.	.	.	*1170*	*3500*
S. pedicellaris	.	.	.	.	.	.	.	.	.	.	.	.	18400
	.	.	.	.	.	.	.	.	.	.	.	.	*1940*
S. petiolaris	1060[d]	8120	2310	1390	.	50	.	.	.	.	.	.	.
	2610	*1420*	*810*	.	.	.	.	.	.	.	.	.	.
S. pseudomonticola	170	6000	.	.	.	1210	330	40	.	.	.	.	.
	.	*2120*	.	.	.	.	.	.	.	.	.	.	.
S. pyrifolia	1440	7380	1310	6360	1140	1180	.	.	.	.	.	.	660
	60	*40*	*1190*	.	.	.	.	.	.	.	.	.	*340*
S. serissima	60	460	60	.	.	.	.	.	.	.	100	2170	1690
	.	.	.	.	.	.	.	.	.	.	.	*500*	*1090*
S. scouleriana	.	.	.	.	.	.	.	.	.	.	500	.	1190
	.	.	.	.	.	.	.	.	.	*40*	*400*	.	*1060*
Myrica gale	.	.	.	.	.	.	.	.	.	.	.	.	64800
	.	.	.	.	.	.	.	.	.	.	.	.	*7750*
Alnus tenuifolia	.	.	60	540	.	.	61300	38300	3500	680	.	6330	1500
	.	.	.	.	.	.	*330*	*960*	*880*	*290*	.	*4330*	*440*
Betula glandulosa	.	.	.	.	.	.	.	.	.	.	.	.	7510
	.	.	.	.	.	.	.	.	.	.	.	.	*1220*
B. papyrifera	.	.	.	20	.	.	670	.	.	70	.	.	.
	.	.	.	.	.	.	.	.	.	*70*	*200*	.	.
B. pumila	.	.	.	.	.	.	.	.	.	.	.	.	5280
	.	.	.	.	.	.	.	.	.	.	.	.	*530*
Ribes hudsonianum	.	.	120	.	.	.	.	.	60	40	.	330	.
	.	.	.	.	.	.	.	.	.	.	.	.	.
R. lacustre	.	.	.	.	.	.	.	.	.	1110	.	.	.
	.	.	.	.	.	.	.	.	.	*110*	.	.	.
R. oxyacanthoides	.	.	.	.	.	.	.	.	190	610	.	170	.
	.	.	.	.	.	.	.	.	.	*110*	.	.	.
R. triste	.	.	.	.	.	.	.	.	750	1000	.	.	.
	.	.	.	.	.	.	.	.	*120*	*110*	.	.	.
Amelanchier alnifolia	.	.	.	.	.	.	.	.	.	1360	.	.	.
	.	.	.	.	.	.	.	.	.	*320*	.	.	.
Rosa acicularis	.	.	60	.	.	.	.	290	10500	17900	.	170	.
	.	.	.	.	.	.	.	.	*940*	*3570*	.	.	.
Rubus strigosus	.	.	.	.	.	.	.	.	1560	1210	.	170	.
	.	.	.	.	.	.	.	.	.	*290*	.	.	.
Shepherdia canadensis	.	.	.	.	.	.	.	.	310	4430	.	5170	.
	.	.	.	.	.	.	.	.	.	*1750*	.	*2830*	.
Cornus stolonifera	.	.	60	.	.	50	.	3290	20200	4430	.	.	.
	.	.	.	.	.	.	.	*40*	*2560*	*960*	.	.	.
Andromeda polifolia	.	.	.	.	.	.	.	.	.	.	.	.	1590
	.	.	.	.	.	.	.	.	.	.	.	.	*120*
Chamaedaphne calyculata	.	.	.	.	.	.	.	.	.	.	.	.	19600
	.	.	.	.	.	.	.	.	.	.	.	.	*1660*
Ledum groenlandicum	.	.	.	.	.	.	.	.	.	.	.	.	7880
	.	.	.	.	.	.	.	.	.	.	.	.	*30*
Symphoricarpos albus	.	.	.	.	.	.	.	.	.	70	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	.	.
Viburnum edule	.	.	.	.	.	.	.	.	690	8430	.	.	.
	.	.	.	.	.	.	.	.	*190*	*360*	.	.	.
Total	2730	32420	19640	59990	81160	22120	88970	73580	41940	43410	12400	35050	137320
	2670	*3660*	*9560*	*880*	.	*30*	*4000*	*2250*	*5000*	*8910*	*5400*	*22500*	*22120*

[a] Dead density given in italicized numbers.
[b] Shrubs include stems greater than 30 cm in height and less than 3 cm in dbh.
[c] Names of community types given in Figure 2; CT's 1-3 have no shrubs.
[d] Values rounded off.

Table 11. Average height (dm) of live shrubs[a], tallied by species in each community type in the study region.

Species	Community Type[b]												
	4	5	6	7	8	9	10	11	12	13	14	15	16
Larix laricina	.	.	.	.	.	.	.	.	.	.	.	.	10
Picea glauca	.	.	.	3	.	.	.	.	.	13	6	9	9[d]
P. mariana	.	.	.	.	.	.	.	.	.	.	.	.	7
Populus balsamifera	.	.	.	7	6	.	.	14	11	9	.	21	.
P. tremuloides	.	4	.	6	.	.	.	.	.	5	11	.	.
Salix arbusculoides	.	23	.	.	.	.	.	.	.	28	23	22	.
S. barklayi (?)	.	.	.	.	.	.	.	.	.	.	.	4	8
S. bebbiana	.	.	29	8	.	8	.	11	6	27	24	19	11
S. glauca	.	.	--	.	.	.	.	.	.	.	.	--	--
S. interior	.	.	.	14	14	5	33	14	.	.	.	.	.
S. lasiandra	.	6	.	.	3	4	.	13	.	.	.	.	.
S. lutea	.	7	.	7	12	4	9	14	.	.	.	.	.
S. myrtillifolia	.	.	.	.	.	.	.	.	.	.	.	22	13
S. pedicellaris	.	.	.	.	.	.	.	.	.	.	.	.	6
S. petiolaris	20	8	55	7	.	3	.	.	.	.	.	.	.
S. pseudomonticola	8	18	.	.	.	11	4	16	.	.	.	.	.
S. pyrifolia	37	6	26	8	10	4	.	.	.	.	.	.	--
S. serissima	--[c]	11	--	.	.	.	.	.	.	.	--	8	9
S. scouleriana	.	.	.	.	.	.	.	.	.	8[d]	15	.	10
Myrica gale	.	.	.	.	.	.	.	.	.	.	.	.	5
Alnus tenuifolia	.	.	--	8	.	.	11	14	18	21	.	20	8
Betula glandulosa	.	.	.	.	.	.	.	.	.	.	.	.	6
B. papyrifera	.	.	.	3	.	.	5	.	.	21	9[d]	.	.
B. pumila	.	.	.	.	.	.	.	.	.	.	.	.	6
Ribes hudsonianum	.	.	--	.	.	.	.	.	7	3	.	6	.
R. lacustre	.	.	.	.	.	.	.	.	.	11	.	.	.
R. oxyacanthoides	.	.	.	.	.	.	.	.	9	6	.	--	.
R. triste	.	.	.	.	.	.	.	.	5	6	.	.	.
Amelanchier alnifolia	.	.	.	.	.	.	.	.	.	10	.	.	.
Rosa acicularis	.	.	--	.	.	.	.	6	7	7	.	6	.
Rubus strigosus	.	.	.	.	.	.	.	.	9	4	.	--	.
Shepherdia canadensis	.	.	.	.	.	.	.	.	8	6	.	7	.
Cornus stolonifera	.	.	--	.	.	5	.	7	12	9	.	.	.
Andromeda polifolia	.	.	.	.	.	.	.	.	.	.	.	.	.
Chamaedaphne calyculata	.	.	.	.	.	.	.	.	.	.	.	.	3
Ledum groenlandicum	.	.	.	.	.	.	.	.	.	.	.	.	6
Symphoricarpos albus	.	.	.	.	.	.	.	.	.	3	.	.	4
Viburnum edule	.	.	.	.	.	.	.	.	14	8	.	.	.
Average (live)	22	10	37	7	9	6	12	12	10	11	16	13	8

a Shrubs include stems greater than 30 cm in height and less than 3 cm in dbh.
b Names of community types given in Figure 2; CT's 1-3 have no shrubs.
c Missing data
d Dead individuals.

Table 12. Average age (yrs) of shrubs[a], tallied by species in each community type in the study region.

Species	Community Type[b]												
	4	5	6	7	8	9	10	11	12	13	14	15	16
Larix laricina	.	.	.	.	.	.	.	.	.	.	.	.	22.9
Picea glauca	.	.	.	10.0	.	.	.	.	.	18.1	11.0	30.3	21.0[c]
P. mariana	.	.	.	.	.	.	.	.	.	.	.	.	28.4
Populus balsamifera	.	.	.	5.2	4.0	.	.	7.8	8.4	20.0	.	12.0	.
P. tremuloides	.	4.0	.	3.0	.	.	.	.	.	23.5	7.5	.	.
Salix arbusculoides	.	22.0[d]	.	.	.	.	.	.	.	10.5	15.7	19.0	.
S. barklayi (?)	.	.	.	.	.	.	.	.	.	.	.	13.0	5.0
S. bebbiana	.	.	11.7	4.1	.	3.2	.	5.5	11.0	13.4	19.0	14.0	32.0
S. glauca	.	.	--[e]	.	.	.	.	.	.	.	.	--	--
S. interior	.	.	.	5.4	5.3[d]	4.0[d]	8.7	8.3	.	.	.	.	.
S. lasiandra	.	6.0	.	.	--	3.0	.	5.5	.	.	.	.	.
S. lutea	.	4.8	.	4.1	5.0	2.8	6.3	5.9	.	.	.	.	.
S. myrtillifolia	.	.	.	.	.	.	.	.	.	.	.	11.0	14.6
S. pedicellaris	.	.	.	.	.	.	.	.	.	.	.	.	6.2
S. petiolaris	13.0	6.1	12.0	--	.	--	.	.	.	.	.	.	.
S. pseudomonticola	24.0	7.5	.	.	.	2.0	3.0	--	.	.	.	.	.
S. pyrifolia	11.0[c]	3.7	14.0	5.9	3.7	2.8	.	.	.	.	.	.	7.0
S. serissima	10.3	7.0	--	.	.	.	.	.	.	.	8.0	13.0	7.0
S. scouleriana	.	.	.	.	.	.	.	.	.	17.0[c]	12.0	.	18.0
Myrica gale	.	.	.	.	.	.	.	.	.	.	.	.	5.2
Alnus tenuifolia	.	.	--	3.2	.	.	3.7	6.5	7.6	10.2	.	10.7	10.7
Betula glandulosa	.	.	.	.	.	.	.	.	.	.	.	.	7.4
B. papyrifera	.	.	.	3.0	.	.	--	.	.	22.5	--	.	.
B. pumila	.	.	.	.	.	.	.	.	.	.	.	.	6.6
Ribes hudsonianum	.	.	5.0	.	.	.	.	.	--	--	.	3.0	.
R. lacustre	.	.	.	.	.	.	.	.	.	4.0	.	.	.
R. oxyacanthoides	.	.	.	.	.	.	.	.	3.0	2.9	.	--	.
R. triste	.	.	.	.	.	.	.	.	4.0	5.5	.	.	.
Amelanchier alnifolia	.	.	.	.	.	.	.	.	.	18.3	.	.	.
Rosa acicularis	.	.	4.0	.	.	.	.	--	4.8	5.1	.	5.0	.
Rubus strigosus	.	.	.	.	.	.	.	.	--	2.0	.	--	.
Shepherdia canadensis	.	.	.	.	.	.	.	.	15.0	12.6	.	14.0	.
Cornus stolonifera	.	.	7.0	.	.	.	.	9.0	11.1	9.2	.	.	.
Andromeda polifolia	.	.	.	.	.	.	.	.	.	.	.	.	--
Chamaedaphne calyculata	.	.	.	.	.	.	.	.	.	.	.	.	5.9
Ledum groenlandicum	.	.	.	.	.	.	.	.	.	.	.	.	6.4
Symphorcarpos albus	.	.	.	.	.	.	.	.	.	--	.	.	.
Viburnum edule	.	.	.	.	.	.	.	.	5.5	6.5	.	.	.
Average (live)	15.8	7.6	9.0	4.9	4.5	3.0	5.4	6.9	7.8	11.5	12.2	13.2	12.2

a Shrubs include stems greater than 30 cm in height and less than 3 cm in dbh.
b Names of community types given in Figure 2; CT's 1-3 have no shrubs.
c Dead individuals
d Representative age: mean of oldest species in the community type.
e Missing data

Table 13. Average density (stems/ha) of live dwarf-shrubs[a], tallied by species in each community type in the study region.

Species	Community Type[b]												
	4	5	6	7	8	9	10	11	12	13	14	15	16
Larix laricina	.	.	.	.	.	.	.	.	.	.	.	.	1750
Picea glauca	.	1080	750	2540	.	630	9330	2500	750	2280	4000	4000	380
P. mariana	.	.	.	.	.	.	.	.	.	.	.	.	1380
Populus balsamifera	.	.	750	2180	860	100	1330	1830	1250	140	.	.	.
P. tremuloides	.	.	.	540	.	.	.	.	.	140	800	.	.
Salix barklayi (?)	.	.	.	.	.	.	.	.	.	.	.	3330	380
S. bebbiana	.	460	3750	2640	570	4420	4670	2830	250	280	800	2000	.
S. interior	.	.	.	5090	4000	6320	5330	4000	.	.	.	.	.
S. lasiandra	.	.	.	270	.	.	.	330	.	.	.	.	.
S. lutea	.	3230	.	5730	2860	6420	4000	2330	.	.	.	.	.
S. myrtillifolia	.	.	.	.	.	.	.	.	.	.	.	2000	880
S. pedicellaris	.	.	.	.	.	.	.	.	.	.	.	.	3500
S. petiolaris	3330[c]	3850	1000	2090	.	.	.	.	.	.	.	.	.
S. pseudomonticola	.	.	.	90	.	.	.	.	.	140	.	.	.
S. pyrifolia	890	3080	.	3270	.	1790	.	.	.	.	.	670	1120
S. serissima	.	.	.	.	.	.	.	.	.	.	.	.	250
Myrica gale	.	.	.	.	.	.	.	.	.	.	.	.	13900
Alnus tenuifolia	.	310	.	460	.	100	8670	3500	1500	710	2000	6670	1250
Betula glandulosa	.	.	.	.	.	.	.	.	.	.	.	1330	2500
B. papyrifera	.	.	.	360	.	.	.	.	.	140	800	670	.
B. pumila	.	.	.	.	.	.	.	.	.	.	.	.	2750
Ribes hudsonianum	.	.	1000	.	.	.	.	.	.	280	.	2000	.
R. oxyacanthoides	.	.	.	.	.	.	.	170	.	2710	.	2000	.
R. triste	.	.	.	.	.	.	.	.	500	280	.	.	.
Amelanchier alnifolia	.	.	.	.	.	.	.	.	.	1280	.	.	.
Rosa acicularis	.	.	.	.	.	.	.	.	6250	12000	.	2000	.
Rubus strigosus	.	.	.	.	.	.	.	830	500	3860	.	670	.
Shepherdia canadensis	.	.	.	.	.	.	.	.	250	2140	.	2670	.
Cornus stolonifera	.	.	.	.	.	320	.	4500	5000	2710	400	670	.
Andromeda polifolia	.	.	.	.	.	.	.	.	.	.	.	.	2000
Arctostaphylos uva-ursi	.	.	.	.	.	.	.	.	.	280	.	2000	250
Chamaedaphne calyculata	.	.	.	.	.	.	.	.	.	.	.	.	4500
Ledum groenlandicum	.	.	.	.	.	.	.	.	.	.	.	.	4750
Vaccinium vitis-idaea	.	.	.	.	.	.	.	.	.	.	.	.	250
Symphoricarpos albus	.	.	.	.	.	.	.	.	.	280	.	.	.
Viburnum edule	.	.	.	.	.	.	.	.	500	13100	.	2000	.
Total	4220	12010	7250	25260	8290	20100	33330	22820	16750	42750	8800	34680	41790

[a] Dwarf shrubs include stems less than 30 cm in height.
[b] Names of community types given in Figure 2; CT's 1-3 have no dwarf shrubs.
[c] Values rounded off.

b. Environment

This CT occurs only along the shoreline of Egg Lake. Its zones are infrequently inundated by over-levee flood-waters which may then remain throughout the summer. Water-level records suggest that this CT is covered by waters for up to one month in years when the study area is not flooded. The duration of flood waters is prolonged by the presence of depressional to level zones where the average height is 0.2 m ASWL, with the range being 0-0.3 m.

The poorly developed, neutral (6.7-7.3) soils of this CT are mostly Gleysols having interbedded organic horizons. The soils have high sodium values; medium conductivity values; and low sulphate, calcium carbonate, and available nitrogen, phosphorus, and potassium values. Sedimentation rates usually are negligible but may increase greatly when channel waters periodically breach the levees surrounding the basin. Deposited textural classes are essentially sandy loams and loams. Clay content is most variable with the sand fraction dominant (50%). The average S/C ratio is 4.0 (range: 2.9-5.0). The upper soil horizons were composed of organic matter in 1970, resulting from *in situ* plant decomposition, with flood-deposited sediments beneath. Organic matter content for the profile is medium, 2nd only to the Bog CT. The mean field soil moisture content of 221% is 2nd only to the Bog CT (range: 63-335%). These values are *ca.* 4x FC

and 8x PWP, indicating a high (high refers to field soil moisture contents $\geq$ FC and >4x PWP) moisture surplus from prevailing influence of the hydrologic regime and very poor drainage in this CT.

c. Integration

This CT occupies the hydric and subhydric segments of the moisture gradient. *Scolochloa festucacea*, *Rorippa islandica*, *Bidens cernua*, and 12 other species in the herb-dwarf shrub stratum achieve their highest mean PV's here (Table 6, App. 9). These species and those exclusive to this CT are categorized as "subhydrophytic".

This CT forms a transition between aquatic and terrestrial environments, and is therefore quite variable in time because of changing factors promoting either aquatic or terrestrial species. During consecutive years of net drawdown, fairly large belts of aquatic vegetation around the periphery of Egg Lake become stranded and dessicated. The resulting mats of dead aquatic plants are rapidly colonized by semi-aquatic sexually reproducing species such as *Rorippa islandica*, *Bidens cernua*, *Carex sychnocephala*, *Ranunculus natans*, and *R. sceleratus* (Table 6). Other species such as *Carex atherodes* and *Scolochloa festucacea* have extensive rhizome systems and also quickly invade the mats. Rhizomatous species exhibit the greatest abundance and vitality, and persisted on organic soils having a moisture content well in excess of FC.

They can withstand frequent drawdowns of considerable duration. Thus frequency, magnitude, and duration of flood waters and drought spells are important in determining the relative abundance and vitality of species in this transitional habitat.

Typical wet meadow species are not insensitive to sedimentation, but appear well-adjusted to the magnitude and texture of suspended loads in the over-levee flood waters which periodically occur in the EL basin. The flushing action of flood waters probably is a rejuvenating factor controlling the pH balance and effectively restricting the invasion of more acidophilic species. Depth and duration of snow and ice may be more important *re*: species occurrences in this CT *cf.* other CT's of this study area except for the Vascular Aquatic CT. Moving ice is generally not an important factor affecting CT's in the area, but on rare occasions it causes severe gouging, displacement, or destruction of vascular aquatic and wet meadow communities.

The extent of this CT is highly dependent upon water levels in the basin. It expands in area during prolonged drawdown periods and contracts after the study area is inundated by flood waters overflowing the levees. Thus, this CT is constantly shifting in location and extent in response to changing environmental factors.

Vegetational and environmental characteristics suggest that this CT is a relatively unstable stage controlled by polygenic factors. This distinct CT is comparable to the Shore Association of Raup (1935), the Emergent and Immature Fen Habitat Type of Townsend (1973b), and the Fen CT of Dirschl *et al.* (1974).

5. *Salix petiolaris/Carex atherodes* (Meadow) CT
Zone # 79-81, 88-90, 96-99, 106, 107, 126 (Fig. 2)

a. Vegetation

This CT is composed of 13 communities located in generally sheltered areas between Marsh and Moist Lowland Forest, and Herb Immature Marsh and Fen CT's in the CS study area, and between Wet Meadow and Fen CT's in the EL study area. This type is very common in the CS area but is much less common in the EL area (Fig. 3). It is most similar to Fen, followed by Marsh and Wet Meadow CT's. Mean similarity among its communities is 63%, the 3rd highest recorded (Table 1). There are no subtypes in this CT (Table 14).

The mean number of vascular species per community is 20 (Table 2). No species are exclusive to this CT but two species in the shrub stratum and three in the herb-dwarf shrub stratum have their highest mean PV's here (Table 14, App. 9). This type has a very poorly developed tree stratum, a poorly developed shrub stratum, and a highly developed herb-dwarf shrub stratum (Pl. 9). This

Table 14. Species prominence in the *Salix petiolaris/Carex atherodes* (Meadow) Community Type.

Study Area	Chilaway Snye								Egg Lake			CS		$\bar{x}$
Site Number	1	2	1	1	3	3	3	2	1	1	3	2	3	
Zone Number	79	88	80	81	97	98	99	89	106	107	126	90	96	
Species Composition														
Tree Stratum: A	.	.	.	1	.	.	.	.	.	.	.	.	.	0.1
Salix arbusculoides	.	.	.	2[a]	.	.	.	.	.	.	.	.	.	0.2
Shrub Stratum: A	5	3	4	5	4	3	4	5	.	2	1	4	.	3.1
Salix petiolaris +	155	23	155	2	200	2	200	19	.	335	2	2	.	84
S. lutea	375	100	155	2	179	3	19	155	.	.	.	.	.	76
S. pyrifolia	126	200	.	.	100	2	100	179	.	.	.	.	.	54
S. pseudomonticola +	.	.	.	2	200	.	.	.	.	2	.	335	.	42
S. arbusculoides	.	.	.	.	.	.	.	.	.	.	.	126	.	9.7
Salix spp.	.	.	.	.	.	.	.	45	.	.	.	45	.	6.9
S. lasiandra	2	.	2	13	.	.	.	.	.	.	.	.	.	1.3
S. serissima	2	.	2	2	.	.	2	.	.	.	.	.	.	0.6
Populus tremuloides	.	.	.	.	.	.	.	3	.	.	.	.	.	0.2
Herb-Dwarf Shrub Stratum: A	26	25	19	14	19	19	20	18	15	17	19	14	17	19
Carex atherodes	200	200	375	375	200	850	375	375	375	200	200	179	375	329
Calamagrostis canadensis	78	2	.	155	200	89	375	200	2	2	2	.	200	100
Sium suave +	100	179	30	3	23	30	27	30	2	3	2	3	3	34
Polygonum amphibium +	63	27	63	179	.	23	2	19	19	2	2	3	.	31
Mentha arvensis	78	78	2	2	100	2	4	2	2	27	2	3	63	28
Eleocharis palustris +	89	4	.	.	200	2	2	.	.	4	.	.	5	24
Scutellaria galericulata	2	23	23	2	2	2	2	3	155	19	19	2	30	22
Salix lutea	100	89	27	3	.	3	2	23	.	.	.	.	.	19
Galium trifidum	3	3	3	23	2	3	78	19	27	5	27	3	23	17
Ranunculus macounii	3	2	.	.	2	2	.	2	2	100	100	.	2	16
Poa palustris	3	23	78	2	23	.	2	2	19	2	27	3	19	16
Glyceria grandis	.	.	.	.	.	.	.	.	2	200	.	.	.	16
Salix pyrifolia	19	30	.	.	23	23	27	78	.	.	.	.	.	15
Equisetum fluviatile	.	.	.	.	23	30	3	.	.	.	.	100	.	12
Stellaria crassifolia	.	2	2	2	.	2	2	2	23	19	89	.	.	11
Picea glauca	2	2	2	.	.	.	.	2	.	2	126	.	.	10
Typha latifolia	.	.	.	.	.	.	.	.	.	.	.	.	126	9.7
Salix petiolaris	23	30	2	2	19	2	23	3	13	2	3	2	.	9.5
Epilobium glandulosum	3	2	3	3	.	2	2	2	2	2	78	2	.	7.8
Polygonum lapathifolium	3	2	.	19	30	2	30	.	.	.	.	.	.	6.6
Salix bebbiana	.	.	.	.	.	.	.	.	.	.	.	78	.	6.0
Beckmannia syzigachne	.	.	.	.	.	.	.	.	.	.	.	.	63	4.8
Ranunculus pensylvanicus	3	13	3	.	2	.	.	.	27	.	.	.	2	3.8
Stachys palustris	4	4	19	2	2	2	.	.	.	2	2	2	2	3.2
Rorippa islandica	2	2	3	.	2	3	.	.	2	.	19	.	.	2.5
Hippuris vulgaris	19	.	3	.	3	2	3	.	.	.	.	.	.	2.3
Potentilla norvegica	.	.	.	.	.	.	23	3	.	2	2	.	.	2.3
Puccinellia nuttalliana	.	23	.	.	.	.	.	.	.	.	.	.	.	1.8
Alnus tenuifolia	.	.	.	.	.	.	.	19	.	.	.	.	.	1.5
Phalaris arundinacea	2	2	3	.	.	.	.	.	.	.	.	.	2	0.7
Carex rostrata	.	.	2	.	2	.	2	.	.	.	.	.	2	0.6
Erigeron lonchophyllus	3	2	3	.	.	.	.	.	.	.	.	.	.	0.6
E. philadelphicus	.	3	.	.	.	.	.	.	.	.	3	.	.	0.5
Juncus balticus	3	.	.	.	.	.	.	.	.	.	.	.	2	0.4
Scirpus validus	.	.	.	.	2	.	.	.	.	.	.	.	2	0.3
Ranunculus natans	.	.	.	.	.	.	.	.	.	.	4	.	.	0.3
Equisetum hyemale	.	.	.	.	.	.	.	3	.	.	.	.	.	0.2
Urtica gracilis	.	.	.	.	.	.	.	.	.	.	3	.	.	0.2
Scholochloa festucacea	2	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Deschampsia caespitosa	2	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Juncus bufonius	2	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Glyceria striata	.	2	.	.	.	.	.	.	.	.	.	.	.	0.2
Geum macrophyllum	.	.	.	.	.	.	2	.	.	.	.	.	.	0.2
G. allipecum	.	.	.	.	.	.	.	.	.	.	.	2	.	0.2
Stellaria longifolia	.	.	.	.	.	.	.	.	.	.	.	2	.	0.2

CS Chilaway Snye study area.
$\bar{x}$ Mean.
A Number of species.
a Prominence value (rounded off).
+ Species achieving their highest prominence values by stratum in this community type.

Plate 9. *Salix petiolaris/Carex atherodes* community in the *S. petiolaris/C. atherodes* (Meadow) Community Type of zone 126 at site #3 of the Egg Lake study area.

CT has the highest mushroom cover but liverworts and lichens are absent (Table 2). Total understory biomass averages 2,800 kg/ha (3rd highest recorded) with graminoids contributing 81% (Table 4). Representative age of this CT is 22 years (Table 12).

Tree Stratum

Average cover of this stratum is 0.04%. The mean number of species per community in this stratum is 0.1, the same as in the Wet Meadow CT (Table 2). *Salix arbusculoides* is the sole species in this stratum (Table 14). No individuals attain tree status in this CT; total live sapling density is 6 stems/ha with no dead individuals present in the quadrats (Table 7). The average height of live individuals is 4.2 m (Table 8). No age data is available (Table 9).

Shrub Stratum

Average shrub cover is 27%. The mean number of species per community in this stratum is 3 (Table 2). *Salix petiolaris* is most prominent, followed very closely by *S. lutea*, *S. pyrifolia*, and *S. pseudomonticola*. The other five species are relatively unimportant in this CT (Table 14). Total live and dead shrub densities are 32,400 and 3,700 stems/ha. *Salix lutea*, *S. petiolaris*, *S. pyrifolia*, and *S. pseudomonticola* provide the main contribution to live density, while *S. pseudomonticola*

and *S. petiolaris* provide most of the dead density (Table 10). This stratum has an average height of 10 dm (Table 11). The average age of live individuals is 8 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 21 forbs, 16 graminoids, 6 woody species, and 2 horsetails (Table 14). The mean number of species per community in this stratum is 19. Average stratum cover is 61%, the 4th highest recorded (Table 2). *Carex atherodes* is the dominant species, followed distantly by *Calamagrostis canadensis*, *Sium suave*, *Polygonum amphibium*, *Mentha arvensis*, *Eleocharis palustris*, *Scutellaris galericulata*, *Salix lutea*, *Galium trifidum*, *Ranunculus macounii*, and *Poa palustris*. Remaining species are unimportant in this CT (Table 14). Total live dwarf-shrub density is 12,000 stems/ha; the major contributors being *Salix petiolaris*, *S. lutea*, and *S. pyrifolia* (Table 13).

b. Environment

This CT occurs only in the lowlands of the CS and EL study areas. The zones have an average height of 0.2 m ASWL (range: 0-0.4 m). This CT is infrequently inundated by over-levee flood waters for about one month during the growing season.

The strongly acid (5.3) to neutral (7.2) soils of this CT are mainly Rego Gleysols and, to a lesser extent, Orthic Gleysols. The soils have high sodium and available potassium values; medium conductivity and available nitrogen values; and low sulphate, calcium carbonate, and available phosphorus values. Sedimentation rates are negligible in most years but may increase when channel waters periodically breach the EL levee or reach isolated locations in the CS basin. The sediments are mostly sandy clay, followed by loam, sandy clay loam, clay loam, sandy loam, and also organic. Clay content is most variable with the sand fraction dominant and averaging 48%. The average S/C ratio is 1.7 (range: 0.9-3.1). Profile organic matter content is low. The topography ranges from depressional to level zones. The mean field soil moisture content of 61% is the 3rd highest recorded (range: 35-165%). These values are *ca*. 1x FC and 2x PWP. These relationships indicate a moderate soil moisture surplus here *cf*. the high surplus in zones of the Wet Meadow CT. This conclusion is substantiated by soil moisture samples taken during the 1971 growing season. Soil moisture content again closely corresponds to water-level fluctuations. Imperfectly drained conditions prevail in this CT.

c. Integration

This CT occupies the subhydric to subhygric range of the moisture gradient. *Salix petiolaris* and *S. pseudomonticola* in the shrub stratum, and *Sium suave*, *Polygonum amphibium*, and *Eleocharis palustris* in the herb-dwarf shrub stratum achieve their highest mean PV's here (Table 14, App. 9). These species are categorized as "subhygrophytic".

The leading species of this CT can tolerate periodic floods of long duration and normally slow drawdown periods. Some plant reactions to prolonged inundation and decreased soil oxygen concentrations included the production of adventitious roots and loss of leaves below the prevailing water level in *Salix* spp.; heteromorphy, multiple branching, and fewer and smaller flowers in *Stachys palustris*, and *Mentha arvensis*. Grasses appear to be more tolerant of flooding and its residual effects than the mints; *Calamagrostis canadensis* and *Poa palustris* showed no adverse effects from summer flooding in the CS study area.

Although the leading species of this CT are very tolerant of wet and imperfectly drained conditions, they are generally sensitive to alluviation, especially by coarse-textured sediments. They also appear to be intolerant of deep shade as most occur in open or lightly shaded areas.

Vegetational and environmental characteristics indicate that this CT is a relatively stable stage in a hydrarch succession controlled by predominantly polygenic factors. This relatively distinct CT is comparable to the Meadow Association of Raup (1935), Sedge Meadow and Grass Meadow Habitat Types of Townsend (1937b), and the Low Shrub CT of Dirschl *et al.* (1974).

6. *Salix bebbiana/S. bebbiana/Carex atherodes* (Fen) CT
Zone # 100, 108-110, 117, 118, 127, 128 (Fig. 2)

a. Vegetation

This CT is composed of 8 communities located in sheltered areas between Meadow and Moist Lowland Forest CT's in the CS area, and between Meadow and Upland Forest, and Wet Meadow and Upland Forest CT's in the EL study area. It has a very limited occurrence in the former but is common in the latter study area (Fig. 3). This type is most similar to the Meadow, followed by Wet Meadow, Marsh, and Moist Lowland Forest CT's. Mean similarity among its communities is 66%, the highest recorded (Table 1). There are no subtypes in this CT (Table 15).

The mean number of vascular species per community is 22 (Table 2). No species are exclusive to this CT but two species in the shrub stratum and 13 in the herb-dwarf shrub stratum achieve their highest mean PV's here (Table 15, App. 9). This type has poorly developed tree and shrub strata and a moderately developed

Table 15. Species prominence in the *Salix bebbiana/S. bebbiana/Carex atherodes* (Fen) Community Type.

Study Area		EL	CS	Egg Lake						x̄
Site Number		1	3	1	3	3	2	1	2	
Zone Number		110	100	108	127	128	117	109	118	
Species Composition										
Tree Stratum: A		1	1	1	1	.	1	.	.	0.6
Salix bebbiana		335[a]	200	850	375	.	675	.	.	304
Shrub Stratum: A		5	1	2	1	1	3	2	1	2.0
Salix bebbiana	+	126	375	675	375	126	.	63	126	233
S. petiolaris		.	.	.	.	.	335	.	.	42
S. pyrifolia		.	.	.	.	.	335	.	.	42
S. serissima		.	.	.	.	.	155	.	.	19
S. glauca	+	.	.	63	.	.	.	.	.	7.9
Ribes hudsonianum		2	.	.	.	.	.	2	.	0.5
Alnus tenuifolia		2	.	.	.	.	.	.	.	0.2
Rosa acicularis		2	.	.	.	.	.	.	.	0.2
Cornus stolonifera		2	.	.	.	.	.	.	.	0.2
Herb-Dwarf Shrub Stratum: A		27	19	16	23	20	25	20	20	21
Carex atherodes	+	375	155	335	4	675	200	675	675	387
Calamagrostis canadensis	+	375	179	.	3	2	2	63	375	125
Scutellaria galericulata	+	23	2	3	3	100	155	100	100	61
Galium trifidum	+	19	2	5	27	3	100	27	27	26
Mentha arvensis		63	2	4	23	2	78	2	2	22
Epilobium glandulosum	+	3	2	4	4	19	63	78	2	22
Geum allepicum	+	.	2	.	.	.	126	2	.	16
Stellaria longifolia	+	3	2	2	.	78	.	27	.	14
Poa palustris		3	19	5	4	2	63	3	2	13
Erigeron philadelphicus	+	78	2	.	2	.	13	2	2	12
Polygonum amphibium		.	3	2	2	2	63	23	2	12
Ranunculus macounii		.	.	30	30	2	2	23	4	11
Polygonum lapathifolium	+	2	.	2	2	63	2	.	2	9.1
Salix bebbiana		3	3	3	27	3	23	.	.	7.8
Potentilla norvegica		4	3	3	2	.	23	3	13	6.4
Stellaria crassifolia		.	.	.	3	.	19	.	23	5.6
Populus balsamifera		.	.	3	.	.	23	.	.	3.2
Anemone canadensis		2	.	.	.	.	.	2	19	2.9
Sium suave		5	2	3	2	2	2	2	4	2.8
Beckmannia syzigachne		.	.	.	2	19	.	.	.	2.6
Fragaria vesca		.	.	.	.	.	.	3	13	2.0
Stachys palustris		2	.	2	2	2	2	2	2	1.8
Geum macrophyllum		3	2	4	2	.	2	.	.	1.6
Urtica gracilis	+	2	.	.	2	2	.	2	2	1.2
Salix petiolaris		2	2	.	.	2	2	.	.	1.0
Equisetum pratense		2	3	.	.	.	.	3	.	1.0
Rorippa islandica		.	.	.	3	3	2	.	.	1.0
Ribes hudsonianum		2	.	.	2	2	.	.	.	0.8
Aster puniceus	+	2	2	.	2	.	.	.	.	0.8
Ranunculus pensylvanicus		.	.	.	.	.	.	3	2	0.6
Arenaria lateriflora		2	.	.	.	2	.	.	.	0.5
Picea glauca		.	2	.	2	.	.	.	.	0.5
Glyceria grandis		.	.	.	.	.	2	.	2	0.5
Petasites vitifolius		3	.	.	.	.	.	.	.	0.4
Rumex mexicanus	+	2	.	.	.	.	.	.	.	0.2
Actaea rubra		2	.	.	.	.	.	.	.	0.2
Cicuta douglasii		2	.	.	.	.	.	.	.	0.2
Heracleum lanatum	+	2	.	.	.	.	.	.	.	0.2
Scolochloa festucacea		.	.	.	.	.	2	.	.	0.2
Ranunculus natans		.	.	.	.	.	2	.	.	0.2
R. sceleratus		.	.	.	.	.	2	.	.	0.2

EL Egg Lake study area.
CS Chilaway Snye study area.
x̄ Mean.
A Number of species.
a Prominence value (rounded off).
\+ Species achieving their highest prominence values by stratum in this community type.

herb-dwarf shrub stratum (Pl. 10). Detritus cover is the highest recorded and liverworts are absent with mushroom cover the same as in the Meadow CT (Table 2). The total understory biomass averages 2,700 kg/ha (4th highest recorded) with graminoids contributing 99% (Table 4). Representative age of this CT is 27 years.

Tree Stratum

Average cover of this stratum is 31%. The mean number of species per community in this stratum is 0.6 (Table 2). ***Salix bebbiana*** is the sole species (Table 15). Total basal areas are 0.7 and 0.6 m^2/ha for live and dead individuals of ***Salix bebbiana***. Only in this CT does dead almost exceed live basal area (Table 16). Total live tree density is 20 stems/ha (Table 17). No dead individuals were recorded in the quadrats. Total live and dead sapling densities are 4,100 and 790 stems/ha (Table 7). Average tree height is 6.1 m (Table 18); average live sapling height is 5.2 m and for dead individuals 4.1 m (Table 8). Average age for live saplings and trees is 27 years (Table 9,19).

Shrub Stratum

Average shrub cover is 37%. The mean number of species per community in this stratum is 2, the 5th lowest recorded (Table 2). ***Salix bebbiana*** is dominant, followed, to a much lesser extent, by ***S. petiolaris*** and

Plate 10. *Salix bebbiana/Carex atherodes* community in the *S. bebbiana/S. bebbiana/C. atherodes* (Fen) Community Type of zone 118 at site #2 in the Egg Lake study area.

Table 16. Average basal area (m^2/ha) of live and dead[a] trees[b], tallied by species in each community type in the study region.

Species	Community Type[c] 6	11	12	13	14	15	16
Larix laricina	.	.	.	.	.	.	0.1
	.	.	.	.	.	.	.
Picea glauca	.	.	0.9	7.0	0.4	1.7	.
	.	.	*0.1*	*0.3*	.	*0.3*	.
P. mariana	.	.	.	.	.	.	0.03
	.	.	.	.	.	.	.
Populus balsamifera	.	1.4	20.8	7.7	0.6	1.2	.
	.	*0.04*	*2.5*	*0.3*	*0.2*	*0.5*	.
P. tremuloides	.	.	.	6.0	5.4	0.2	.
	.	.	.	*0.7*	.	.	.
Salix arbusculoides	.	.	.	0.2	.	0.5	.
	.	.	.	*0.7*	.	*0.5*	.
S. bebbiana	0.7	1.3	0.5	3.4	4.4	.	.
	0.6	*0.2*	.	*1.5*	*0.9*	.	.
S. scouleriana	.	.	.	.	0.3	.	.
	.	.	.	.	*0.2*	.	.
Alnus tenuifolia	.	1.2	5.9	0.5	.	0.3	.
	.	*0.4*	*0.9*	*0.1*	.	.	.
Betula papyrifera	.	.	0.1	1.2	0.1	0.3	.
	.	.	.	*0.6*	.	.	.
Total	0.7	3.9	28.2	26.0	11.2	4.2	0.1
	0.6	*0.6*	*3.5*	*4.2*	*1.3*	*1.3*	.

[a] Dead basal area given in italicized numbers.
[b] Trees include stems greater than 8 cm dbh.
[c] Names of community types given in Figure 2; CT's 1-5, 7-10 have no trees.

Table 17. Average density (stems/ha) of live and dead[a] trees[b], tallied by species in each community type in the study region.

Species	Community Type[c] 6	11	12	13	14	15
Picea glauca	.	.	30	320	16	213
	.	.	.	*6*	.	.
Populus balsamifera	.	60	670	320	16	.
	.	.	*70*	*23*	*16*	*27*
P. tremuloides	.	.	.	606	528	.
	.	.	.	*40*	.	.
Salix arbusculoides	.	.	.	17	.	27
	.	.	.	*69*	.	.
S. bebbiana	20	140	70	269	176	.
	.	*7*	.	*57*	.	.
S. scouleriana	.	.	.	6	32	.
	.	.	.	.	.	.
Alnus tenuifolia	.	20	520	11	.	27
	.	.	*10*	*6*	.	.
Betula papyrifera	.	.	10	91	.	.
	.	.	.	*46*	.	.
Total	20	220	1300	1640	768	267
	.	*7*	*80*	*247*	*16*	*27*

a Dead density given in italicized numbers.
b Trees include stems greater than 8 cm dbh.
c Names of community types given in Figure 2; CT's 1-5, 7-10, 16 have no trees in the quadrats

Table 18. Average height (m) of live and dead[a] trees[b], tallied by species in each community type in the study region.

Species	Community Type[c] 6	11	12	13	14	15
Picea glauca	.	.	3.2	15.5	---	9.2
	.	.	.	*11.9*	.	.
Populus balsamifera	.	11.2	21.3	14.8	11.6	.
	.	.	*12.1*	*8.7*	*6.6*	*6.8*
P. tremuloides	.	.	.	14.7	15.3	.
	.	.	.	*8.3*	.	.
Salix arbusculoides	.	.	.	8.7	.	4.3
	.	.	.	*7.0*	.	.
S. bebbiana	6.1	8.6	12.4	7.0	4.9	.
	.	*6.1*	.	*5.2*	.	.
S. scouleriana	.	.	.	---[d]	6.6	.
	.	.	.	.	.	.
Alnus tenuifolia	.	8.0	9.0	6.1	.	8.6
	.	.	*6.7*	*8.3*	.	.
Betula papyrifera	.	.	3.0	11.3	.	.
	.	.	.	*3.0*	.	.
Average	6.1	9.3	9.8	11.2	9.6	7.4
	.	*6.1*	*9.4*	*7.5*	*6.6*	*6.8*

a Dead individuals given in italicized numbers.
b Trees include stems greater than 8 cm dbh.
c Names of community types given in Figure 2; CT's 1-5, 7-10, 16 have no trees in the quadrats.
d Missing data.

Table 19. Average age (yrs) of trees[a], tallied by species in each community type in the study region.

Species	Community Type[b]						
	6	11	12	13	14	15	16
Larix laricina	.	.	.	.	.	.	80[c]
Picea glauca	.	.	137[c]	145[c]	45	83[c]	.
P. mariana	.	.	.	.	.	.	77
Populus balsamifera	.	26	130	98	27	---	.
P. tremuloides	.	.	.	82	73[c]	.	.
Salix arbusculoides	.	.	.	---	.	---	.
S. bebbiana	27[c]	32	28	64	45	.	.
S. scouleriana	.	.	.	33	61[e]	.	.
Alnus tenuifolia	.	39[c]	45	26	.	26	.
Betula papyrifera	.	.	---[d]	100	.	.	.
Average age (live)	27	32	85	78	48	54	78

a Trees include stems greater than 8 cm dbh.
b Names of community types given in Figure 2; CT's 1-5, 7-10 have no trees.
c Representative age: mean of oldest species in the community type.
d Missing data
e Dead individuals

S. pyrifolia. The other six species are unimportant in this CT (Table 15). Total live and dead shrub densities are 19,600 and 9,600 stems/ha, contributed mainly by *S. bebbiana* (Table 10). The average height of live individuals is 37 dm (Table 11); the average age of live individuals is 9 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 29 forbs, 6 graminoids, 5 woody species, and 1 horsetail (Table 15). The mean number of species per community in this stratum is 21, the same as in the Wet Meadow CT. Stratum cover averages 59% (Table 2). *Carex atherodes* is the overwhelming dominant, its PV being *ca*. 3x and 6x those of the next two species, *Calamagrostis canadensis* and *Scutellaria galericulata*. The next 9 species fall into the 10-30 PV range, while the remainder are uncommon in this CT (Table 15). Total live dwarf-shrub density is 7,200 stems/ha (5th lowest recorded) with young *Salix bebbiana* the major contributor (Table 13).

b. Environment

This CT occurs only in the lowlands of the CS and EL basins and is not extensive in either. The zones have an average height of 0.4 m ASWL and a range of 0.2-0.5 m. The zones are infrequently inundated by over-levee flood waters. When not flooded, waters may remain for up to one

month during the growing season.

The medium acid (5.8) to moderately alkaline (7.9) soils of this CT are all Orthic Gleysols. The soils have high sodium and available nitrogen values; medium conductivity and calcium carbonate values; and low sulphate and available phosphorus and potassium values. Sedimentation rates are negligible. Soil textures are mostly sandy loam, followed by loam and sandy clay loam. Clay content is most variable, with the sand fraction dominant and averaging 54%. The average S/C ratio is 4.2 (range: 2.1-8.1). Average profile organic content is medium. The topography ranges from depressional to very gently sloping zones. The mean field soil moisture content of 51% is the 4th highest recorded (range: 33-94%). These values are *ca*. 1x FC and 3x PWP. These relationships indicate a moderate soil moisture surplus resulting from the prevailing influence of the hydrologic regime. This conclusion is substantiated by soil samples taken during the 1971 growing season. The extreme variability in the soil moisture regime probably reflects the close correspondence to water-level fluctuations. Imperfectly drained conditions predominate in this CT.

c. Integration

This CT occupies the hygric to mesic range of the moisture gradient. *Salix bebbiana* and *S. glauca* in the shrub stratum, and *Carex atherodes*, *Calamagrostis canadensis*, *Scutellaria galericulata*, and 10 other species in the herb-dwarf shrub stratum achieve their highest mean PV's in this CT (Table 15, App. 9). These species are categorized as "subhygrophytic".

Species having their highest prominence in this CT, like those of the previous CT, are sensitive to alluviation but very tolerant of wet, imperfectly drained conditions occurring in open and lightly shaded areas.

Differences in the vitality and production of adventitious roots in *Salix* spp. in the Meadow and Fen CT's between CS and EL study areas are quite apparent. These differences are related to variations in duration of flooding and drawdown periods in these areas. The relatively poor vigor and vitality of *Salix* spp. in the EL basin seem directly related to the stagnation of flood waters as numerous individuals had abundant adventitious roots measuring over 20 cm in length. This relationship was previously noted by Kramer (1951) who suggested that there is a positive correlation between the development of adventitious roots and the extent of injury or death of the original root system. The adventitious roots allow *Salix* spp. to tolerate increased soil oxygen deficiency

during the prolonged flood periods while absorbing water and nutrients when previous flood injury has occurred to the original root system. These new roots, although keeping individuals barely alive, can not maintain the former vigor of *Salix* spp. if more floods occur, eventually leading to death of the willows and disappearance or upslope displacement of the zone.

Salix spp. are better adapted to partial and complete inundation for extended periods than most other woody species in the boreal landscape (Putnam 1951, Brink 1954, Hosner 1958). However, *Salix* spp. are susceptible to certain types of flooding and drawdown cycles. For example, Harris and Marshall (1963) showed that *Salix* spp. had died in areas subject to 1 and 2 years of drawdown followed by 2 or 3 years of moderately deep flooding. A drawdown of 4 and 5 years permitted *Salix* spp. to survive after 3 years of reflooding to a depth of *ca.* 30 cm. However, very high mortality occurred during the 4th year in over 25 cm with complete mortality occurring after 4 years in more than 61 cm and after 5 years in 46 cm. It is entirely possible that these sublethal and lethal cycles have occurred in the EL basin as evidenced by the numerous dead *Salix* clumps in Vascular Aquatic, Wet Meadow, Meadow, and Fen CT's. Over-levee spring flooding of the basin in 1971 to a depth of *ca.* 1.5 m reduced the abundance and vitality of many fen species, including

Carex atherodes and *Calamagrostis canadensis*, but apparently had no serious effects on mature *Salix* individuals. It is probable that susceptibility and, therefore, mortality rates vary with age of *Salix* spp.

Harris and Marshall (1963) showed that *Carex* spp. had reduced abundance and vitality if the water depth was over 30 cm in the third year of reflooding and died out completely if these water levels were maintained into the fourth year. Similar trends were noted in *C. atherodes* during the first year of flooding which produced 1972 water levels *ca*. 75 cm higher than those in 1971.

Vegetational and environmental characteristics indicate that this CT is a relatively stable stage controlled by polygenic factors. This relatively distinct CT is comparable to the Tree Association of Raup (1935), the Tall Shrub Habitat Type of Townsend (1973b), and the Tall Shrub CT of Dirschl *et al*. (1974).

7. *Salix lutea/Carex atherodes* (Marsh) CT
   Zone # 53-57, 61-66, 69-75, 77, 78, 86, 87 (Fig. 2)

a. Vegetation

This CT is composed of 22 communities located in generally exposed areas behind Algal Aquatic and Shrub Immature Marsh CT's in the LAM study area and between Vascular Aquatic and Meadow CT's in the CS study area. It is very common in the LAM but quite limited in the CS study area (Fig. 3). It is most similar to the Meadow,

followed by Fen, Shrub Immature Marsh, and Swale Shrub CT's. Mean similarity among its communities is 55% (Table 1). No subtypes are recognized in this CT (Table 20).

The mean number of vascular species per community is 32, the 2nd highest recorded (Table 2). Nine species in the herb-dwarf shrub stratum are exclusive to this CT, and three species in the shrub stratum and 19 in the herb-dwarf shrub stratum have their highest mean PV's here (Table 20, App. 9). This type has a very poorly developed tree stratum, a poorly developed shrub stratum, and a highly developed herb-dwarf shrub stratum (Pl. 11). This CT has the 3rd highest moss cover, the same mushroom cover as in the Meadow CT, and no lichens (Table 2). Total understory biomass averages 690 kg/ha (4th lowest recorded) with graminoids (42%) and shrubs (38%) contributing most of the weight (Table 4). Representative age of this CT is 21 years (Table 9).

Tree Stratum

Average tree cover is only 1%. The mean number of species per community in this stratum is 0.1, the same as in the Wet Meadow CT (Table 2). *Salix bebbiana* is the sole member of this stratum and has a very low PV of 7 (Table 20). No individuals attain tree diameter. Total live sapling density is 22 stems/ha with no dead individuals present in the

Table 20. Species prominence in the *Salix lutea/Carex atherodes* (Marsh) Community Type.

Study Area	Lake Athabasca Marsh																		Chilaway Snye				$\bar{x}$
Site Number	2	2	3	3	3	2	2	2	3	3	3	3	2	1	1	1	1	1	1	2	2	1	
Zone Number	66	65	69	70	71	64	63	62	72	75	73	74	61	57	56	55	54	53	78	86	87	77	
Species Composition																							
Tree Stratum: A	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	0.1
Salix bebbiana	.	.	.	.	.	.	89a	.	.	.	.	.	.	.	63	.	.	.	.	.	.	.	6.9
Shrub Stratum: A	3	4	6	5	4	3	3	6	5	6	4	4	3	5	3	2	2	4	4	3	5	4	4.0
Salix lutea +	89	155	155	200	179	375	63	126	23	13	19	89	200	179	2	30	30	30	200	69	200	200	120
S. interior	100	100	200	3	89	200	375	200	19	23	200	100	375	200	375	3	4	3	.	.	.	.	117
S. bebbiana	.	.	.	.	.	.	19	200	200	375	200	375	.	200	126	.	.	.	.	.	.	.	77
S. pyrifolia +	63	23	155	200	179	155	.	.	.	.	.	.	.	.	.	.	.	2	200	100	200	.	58
S. petiolaris	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	2	78	27	100	89	14
Alnus tenuifolia	.	.	.	.	.	.	.	13	13	126	13	.	.	13	.	.	.	.	63	.	.	.	11
Populus balsamifera	.	63	19	4	13	.	.	19	.	.	.	19	.	13	.	.	.	.	.	.	3	19	7.8
Salix spp. +	.	.	.	.	.	.	.	.	.	155	.	.	.	.	.	.	.	.	.	.	.	.	7.0
Populus tremuloides	.	.	13	13	.	.	.	19	2	3	.	.	.	.	.	.	.	.	.	.	3	.	2.4
Picea glauca	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.1
Betula papyrifera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	0.1
Herb-Dwarf Shrub Stratum: A	29	31	46	39	32	32	34	43	40	30	26	20	27	28	29	24	24	22	32	26	33	35	31
Carex atherodes	200	63	78	200	30	200	19	100	200	155	200	200	126	89	179	179	30	23	200	23	89	89	121
Phragmites communis +	100	200	100	2	200	100	3	100	2	.	19	.	200	200	19	.	375	2	.	.	.	.	74
Salix lutea +	126	2	3	89	89	2	3	3	2	2	3	3	4	3	3	3	200	27	200	89	63	100	46
Deschampsia caespitosa +	78	179	63	27	30	2	2	19	23	.	.	.	.	.	3	200	2	100	89	19	19	23	40
Mentha arvensis +	3	23	.	23	19	2	3	2	179	3	23	23	19	3	3	.	2	3	200	5	200	100	38
Calamagrostis canadensis	.	.	3	179	.	2	3	19	89	23	4	100	19	126	3	.	.	.	2	19	200	.	36
Salix interior	200	19	23	2	27	13	200	3	4	2	27	4	23	19	30	3	2	3	.	.	.	.	27
Carex aquatilis	63	.	19	2	2	.	.	2	2	63	2	179	200	3	27	2	2	.	.	.	.	.	26
Phalaris arundinacea	.	.	2	2	2	2	.	2	2	.	.	.	2	19	.	.	100	2	89	.	200	23	20
Salix pyrifolia +	3	3	30	100	89	.	.	.	.	.	.	.	.	.	3	.	.	.	89	.	27	100	20
Ranunculus macounii +	2	19	2	2	23	27	3	78	23	13	2	2	2	100	2	3	2	13	3	78	2	23	19
Hordeum jubatum +	3	2	89	19	2	63	3	3	155	.	.	.	.	.	.	2	.	.	.	.	19	19	17
Polygonum amphibium	.	.	78	3	.	.	.	3	27	2	19	27	.	63	2	3	.	.	89	27	30	.	17
Eleocharis palustris	3	2	3	23	.	.	.	2	2	.	2	2	19	.	3	2	2	179	3	78	23	23	17
Poa palustris +	2	2	.	.	3	19	3	2	23	23	23	19	2	.	3	23	2	78	3	19	89	27	17
Beckmannia syzigachne +	63	45	78	19	3	27	.	63	.	.	.	.	2	.	.	2	2	19	2	19	19	2	17
Aster pansus *	3	.	2	23	13	89	3	179	2	.	.	.	.	.	.	.	19	.	.	.	.	.	15
Plantago major +	.	.	27	89	89	.	3	27	27	19	.	.	.	27	.	.	.	.	.	.	23	3	15
Salix bebbiana	.	.	.	.	.	3	27	3	100	63	30	4	.	3	100	.	.	.	.	.	.	.	15
Erigeron lonchophyllus +	3	179	3	3	19	4	3	100	3	.	.	.	.	.	.	.	2	2	2	.	2	3	15
Sium suave	.	.	2	19	23	2	2	2	27	3	27	30	2	3	2	3	3	30	27	89	27	3	15
Typha latifolia	63	.	2	.	.	.	.	.	.	.	3	3	200	.	13	.	.	.	.	.	.	.	13
Artemisia campestris *	.	2	27	2	3	13	2	200	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
Galium trifidum	.	2	.	.	.	.	.	2	2	3	.	.	3	126	3	.	.	.	3	5	89	3	11
Scirpus validus	27	.	.	.	.	.	179	3	.	.	.	.	2	3	.	.	.	.	.	23	.	.	11
Artemisia biennis	2	155	.	4	3	27	27	3	2	.	.	.	.	.	.	2	2	.	.	.	.	.	10
Vicia americana +	.	.	.	.	.	.	.	.	.	200	.	.	.	.	.	.	.	.	.	.	.	.	9.1
Argostis scabra +	.	23	19	.	.	.	.	78	.	63	.	.	.	.	.	.	.	.	.	.	.	.	8.3
Eleocharis acicularis	2	19	2	3	.	.	2	2	.	.	.	.	2	19	.	.	.	78	2	2	.	27	7.3
Carex sychnocephala	19	13	2	.	2	3	2	3	19	.	.	.	.	.	.	.	.	.	.	23	.	63	6.8
Puccinellia nuttalliana +	78	23	3	2	2	3	2	3	2	.	.	.	3	4	.	.	.	.	.	.	.	23	6.7
Epilobium glandulosum	3	19	19	5	4	4	4	19	23	.	3	.	.	4	4	3	27	3	2	.	2	.	6.7
Alnus tenuifolia	.	.	.	.	.	.	.	.	3	126	.	.	.	.	.	.	.	.	13	.	.	.	6.4
Juncus nodosus +	.	.	78	2	3	.	3	.	2	.	.	.	.	19	3	2	2	13	.	2	.	4	6.0
J. alpinus	3	.	78	.	.	.	.	.	.	.	.	.	2	2	19	19	.	.	2	.	.	2	5.8
Equisetum arvense	2	2	3	19	19	3	2	19	23	4	3	2	.	.	.	.	.	.	.	.	.	.	4.6
Rorippa islandica	3	2	19	19	.	.	.	19	.	.	3	.	2	27	.	3	.	.	.	.	2	.	4.5
Scutellaria galericulata	.	.	2	.	.	.	.	.	3	4	.	.	.	3	2	23	2	2	2	3	30	19	4.3
Potentilla norvegica	3	19	3	3	.	19	3	3	4	3	23	.	2	.	2	.	2	2	.	.	.	.	4.1
Equisetum palustre	.	.	.	.	.	.	.	45	.	.	.	.	3	19	2	.	3	2	.	.	.	.	3.4
Salix petiolaris	.	.	2	2	.	.	2	3	2	.	2	3	.	.	.	.	.	.	3	27	4	23	3.3
Epilobium angustifolium	.	.	.	.	.	3	3	3	.	63	.	.	.	.	.	.	.	.	.	.	.	.	3.3
Stachys palustris	.	.	.	.	.	.	.	.	2	2	2	2	.	2	2	2	2	2	2	23	23	2	3.1
Taraxacum officinale *	.	13	2	27	19	.	.	.	3	.	.	.	3	2	.	.	.	.	.	.	.	.	3.1
Carex retrorsa	.	.	.	.	.	.	.	63	.	.	.	.	.	.	.	.	.	.	.	2	.	2	3.0
Limosella aquatica	.	19	2	2	2	.	.	.	3	.	.	.	27	.	.	.	.	.	.	.	.	.	2.5
Populus balsamifera	.	2	2	19	3	3	3	2	3	3	3	3	.	2	.	.	.	.	.	.	3	3	2.4
Hippuris vulgaris +	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	28	3	19	4	2.4
Picea glauca	.	.	2	13	3	3	3	2	4	4	3	.	.	.	.	2	.	.	2	.	3	2	2.1
Equisetum fluviatile	.	.	.	.	.	.	.	.	.	19	3	23	.	.	.	.	.	.	.	.	.	.	2.0
Erigeron philadelphicus	.	13	.	.	.	.	.	23	.	2	.	.	.	.	2	2	.	.	.	.	.	.	1.9
Juncus bufonius	.	.	4	.	.	.	.	.	.	.	.	.	.	.	2	.	.	4	2	.	27	2	1.9
J. balticus	.	13	3	.	.	3	2	.	.	.	.	.	.	.	.	.	2	2	2	2	2	2	1.5
Polygonum aviculare *	2	2	.	.	2	19	2	3	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1.4
Ranunculus pensylvanicus	.	.	.	2	.	2	2	19	.	.	.	.	.	.	.	2	2	.	.	.	3	.	1.4
Populus tremuloides +	.	.	.	.	23	.	.	.	3	3	.	.	.	.	.	.	.	.	.	.	.	.	1.3
Carex bebbii +	.	.	.	.	.	.	.	.	.	.	.	.	.	19	.	.	.	.	2	2	2	2	1.2
Betula papyrifera	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19	1.0
Salix lasiandra +	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.9
Sparganium angustifolium	.	.	.	.	.	.	.	.	.	.	.	.	19	.	.	.	.	.	.	.	.	.	0.9
Phleum pratense *	.	.	2	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	2	2	2	2	0.6
Salix pseudomonticola	.	.	.	.	.	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.6
Potentilla anserina	2	2	2	2	.	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	0.6
Stellaria longifolia	.	.	4	.	2	2	.	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	0.6
Solidago graminifolia +	.	.	3	2	2	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.	0.5
Rumex maritimus	.	.	2	2	.	.	.	.	.	.	.	.	2	2	2	.	.	.	.	.	.	.	0.4
Chenopodium album *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	2	0.4
Potentilla palustris	.	.	.	.	.	.	.	.	2	.	2	2	.	.	.	.	.	.	.	.	.	.	0.3
Stellaria crassifolia	.	.	.	.	.	.	.	.	.	.	2	2	.	.	2	.	.	.	.	.	.	.	0.3
Dracocephalum nuttallii *	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	3	.	0.3
Melilotus alba	.	.	2	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.3
Senecio congestus	.	.	2	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Ranunculus cymbalaria	.	.	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Equisetum pratense	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	0.2
Alopecurus aequalis	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	0.2
Glyceria striata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	0.2
Geum allepicum	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	0.1
Achillea millefolium	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	0.1
Scholochloa festucacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	0.1
Carex rostrata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	0.1
Equisetum laevigatum *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	0.1
Ranunculus flammula *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	0.1

$\bar{x}$ Mean.
A Number of species.
a Prominence value (rounded off).
\+ Species achieving their highest prominence values by stratum in this community type.
* Species by stratum exclusive to this community type.

Plate 11. *Salix bebbiana/S. interior/Carex atherodes* community in the *S. lutea/C. atherodes* (Marsh) Community Type of zone 56 at site #1 in the Lake Athabasca Marsh study area.

quadrats (Table 7). Average height is 2.9 m (Table 8) and average age is 21 years (Table 9).

Shrub Stratum

Average shrub cover is 34%. The mean number of species per community in this stratum is 4 (Table 2). *Salix lutea* is the most prominent of 11 species, followed closely by *S. interior* and, to a lesser extent, *S. bebbiana* and *S. pyrifolia* (Table 20). Total live and dead shrub densities are 60,000 and 880 stems/ha. *Salix interior* provides about half the live density and most of the dead density (Table 10). This stratum has an average height of 7 dm (Table 11). The average age of live individuals is 5 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 37 forbs, 28 graminoids (highest recorded), 12 woody species, and 5 horsetails (highest recorded; Table 20). The mean number of species per community in this stratum is 31, the highest recorded. Average cover of this stratum is 61%, the same as in the Meadow CT (Table 2). *Carex atherodes* is most prominent, followed by *Phragmites communis* and, to a much lesser extent, by *Salix lutea*, *Deschampsia caespitosa*, *Mentha arvensis*, *Calamagrostis canadensis*, *Salix interior*, and *Carex aquatilis*. The next 18 species fall into the 10-20 PV range, while the remainder are unimportant in

this CT (Table 20). *Aster pansus*, *Artemisia campestris*, *Taraxacum officinale*, and six other herb species are exclusive to this CT (Table 20, App. 9). Total live dwarf-shrub density is 25,300 stems/ha, with major contributions from *S. lutea* and *S. interior* (Table 13).

b. Environment

This CT occurs on levee crests, lowlands between levees, and areas adjacent to Precambrian knolls in the LAM study area and on levee crests in the CS study area. Its flood prone zones are frequently flooded, with an average height of 0.5 m ASWL and a range of 0-1.4 m. This CT may be inundated for up to three months during the growing season.

The medium acid (5.8) to mildly alkaline (7.8) soils are mostly Gleyed Regosols. The soils have medium sodium, calcium carbonate, and available potassium values and low conductivity, sulphate, and available nitrogen and phosphorus values. Sedimentation rates are high and vary widely. Deposited sediments are mostly loam followed, to a lesser extent, by sandy loam, sandy clay loam, sandy clay, clay, and clay loam. Clay content is most variable and sand is the dominant fraction, averaging 49%. The average S/C ratio is 2.7 (range: 0.9-4.4). Average profile organic content is low. The topography is depressional to greatly sloping. The mean field soil moisture content is 34% (range: 27-43%). These values

are slightly less than FC and are *ca.* 3x PWP, indicating a moderate soil moisture surplus. Samples taken throughout the growing season indicate a great influence of the hydrologic regime, especially during the spring. Poorly drained conditions prevail in this CT.

c. Integration

This CT occupies the subhydric to subhygric range of the moisture gradient. *Salix lutea*, *S. pyrifolia*, and *Salix* spp. in the shrub stratum, and *Phragmites communis*, *Salix lutea*, *Deschampsia caespitosa*, and 16 other species in the herb-dwarf shrub stratum achieve their highest mean PV's here (Table 20, App. 9). These species and those exclusive to this CT are categorized as "subhygrophytic".

These species achieve the highest prominence in this CT because they are able to tolerate flood waters of long duration and variable drawdown periods. Differences in micro-topography and drainage probably account for zonal variations in species structures and abundances in this CT. Species such as *Vicia americana*, *Puccinellia nuttalliana*, and *Populus tremuloides* occur in higher and drier sections having coarser-textured and better-aerated soils; although capable of tolerating some flooding they appear to be severely restricted by reducing conditions in the soils. On the other hand, species such as *Phragmites communis*, *Deschampsia caespitosa*, and *Beckmannia syzigachne*

are concentrated in lower and wetter sections having finer-textured and less-aerated soils; they appear more tolerant of oxygen deficits. Grasses are generally more tolerant of flooding than most marsh plants. Experiments performed by McKenzie (1951) indicate that *Phleum pratense* is not seriously affected by prolonged flooding as its seeds, seedlings, and mature plants have different flood duration tolerance of 21-56, 21-35, and 49-63 days respectively.

Most of the species of this CT are shade intolerant but a few, like *Equisetum pratense*, are shade tolerant. Best development of the CT occurs in areas sheltered behind strand-line log accumulations. These areas have fewer species of the Herb and Shrub Immature Marsh CT's and more mesic upland species.

Species in the more flood-susceptible zones of this CT must tolerate high sedimentation rates. Measured sediment accumulations from the 1971 flood season averaged *ca.* 3 cm, decreasing with distance back from the levees, such that higher and more isolated areas were sediment-free. Clones of *Phragmites communis* had *ca.* 2 cm of sediment accumulation in the periphery but negligible to trace amounts in the centre. This species' rhizomes appear able to rapidly stabilize these unevenly deposited sediments thus creating potential colonization sites for more mesophytic species. The contagious disper-

sion pattern exhibited by *P. communis* clones may be perpetuated by snow accumulation around old emergent shoots which reduce the loss of ground heat such that fewer rhizomes are killed by freezing. Survival of these rhizomes permits vegetative expansion of a few shoots into larger clumps (Kadlec 1962, Halsam 1972). Species of lower stature inhabit the areas between the clumps and are better adapted to withstand freezing of their root systems, but are more likely to be uprooted by ice as water levels rise in early spring.

Vegetational and environmental characteristics suggest that this CT is a relatively unstable stage controlled and maintained by allogenic factors. This relatively distinct CT is comparable to the Meadow and Shrub Associations of Raup (1935), the Low Shrub Habitat Type of Townsend (1973b), and the Fen and Low Shrub CT's of Dirschl *et al.* (1974).

8. *Salix interior/Typha latifolia* (Shrub Immature Marsh) CT
Zone # 50-52, 58, 60, 67, 68 (Fig. 2)

a. Vegetation

This CT is composed of 7 communities located in generally exposed locations between Algal Aquatic or Herb Immature Marsh and Marsh CT's, and occurs on a limited basis only in the LAM study area (Fig. 3). It is most similar to the Marsh and, secondarily, to the Levee Herb CT's. Mean similarity among its communities is 54%

(Table 1). There are no subtypes in this CT (Table 21).

The mean number of vascular species per community is 16 (Table 2). No species is exclusive to this CT, but five herbs have their highest mean PV's here (Table 21, App. 9). This type has a very poorly developed shrub stratum and a poorly developed herb-dwarf shrub stratum (Pl. 12). This CT has the 3rd lowest detritus and the 4th lowest moss covers, and no mushrooms, lichens, and trees (Table 2). The total biomass averages 391 kg/ha (3rd lowest recorded) with graminoids (44%) and shrubs (28%) contributing most of the weight (Table 4). Representative age is 5 years, the 5th youngest CT (Table 12).

Shrub Stratum

Average shrub cover is 20%, the 5th lowest recorded. The mean number of species per community in this stratum is 3, the same as the Meadow CT (Table 2). ***Salix interior*** is dominant, followed by ***S. lutea*** and ***S. pyrifolia***. The other two species are unimportant in this CT (Table 21). Total live shrub density is 81,200 stems/ha, the major contributor being ***S. interior***. No dead individuals are present in the quadrats (Table 10). This stratum has an average height of 9 dm (Table 11), and an average live age of only 4 years (Table 12).

Table 21. Species prominence in the *Salix interior/Typha latifolia* (Shrub Immature Marsh) Community Type.

Study Area	Lake Athabasca Marsh							$\bar{x}$
Site Number	1	1	1	3	3	2	1	
Zone Number	52	51	50	68	67	60	58	
Species Composition								
Shrub Stratum: A	3	4	2	3	2	2	3	2.7
Salix interior	30[a]	200	200	200	30	100	200	137
S. lutea	100	200	27	27	3	5	30	56
S. pyrifolia	63	63	.	13	.	.	.	20
Populus balsamifera	.	27	.	.	.	.	.	3.9
Salix lasiandra	.	.	.	.	.	.	19	2.7
Herb-Dwarf Shrub Stratum: A	15	16	14	24	10	12	16	15
Typha latifolia	.	200	19	30	23	200	89	80
Eleocharis acicularis +	100	30	89	2	100	.	.	46
Phalaris arundinacea +	126	2	3	30	.	.	2	23
Carex atherodes	30	.	.	.	.	126	.	22
Deschampsia caespitosa	100	2	23	.	.	30	.	22
Carex retrorsa	.	23	4	2	2	.	100	19
Salix interior	3	2	3	3	.	3	100	16
Eleocharis palustris	2	2	3	2	78	19	.	15
Juncus alpinus	.	.	.	27	2	23	23	11
Scirpus validus	.	3	3	3	23	27	2	8.7
Carex aquatilis	.	.	3	30	4	3	19	8.4
Equisetum palustre	2	27	2	3	.	.	.	4.9
Phragmites communis	2	3	.	2	.	.	27	4.9
Carex sychnocephala	.	.	.	2	2	.	30	4.9
Salix lutea	4	4	2	.	.	.	23	4.7
Beckmannia syzigachne	3	3	.	2	.	23	.	4.4
Limosella aquatica +	.	.	2	23	.	.	.	3.6
Equisetum arvense	19	.	.	.	.	.	3	3.1
Senecio congestus +	.	2	2	2	2	.	.	1.1
Juncus nodosus	3	3	2	.	.	.	.	1.1
Triglochin maritima +	.	.	.	2	2	3	.	1.0
Rumex maritimus	.	.	.	2	.	2	2	0.9
Mentha arvensis	3	.	.	.	.	.	3	0.9
Populus balsamifera	3	2	.	.	.	.	.	0.7
Sparganium angustifolium	.	.	.	.	.	3	2	0.7
Salix bebbiana	.	3	.	.	.	.	.	0.4
Hordeum jubatum	.	.	.	3	.	.	.	0.4
Equisetum fluviatile	.	.	.	.	.	.	3	0.4
Calamagrostis canadensis	.	.	.	.	.	.	3	0.4
Solidago graminifolia	2	.	.	.	.	.	.	0.3
Juncus balticus	.	.	.	2	.	.	.	0.3
J. bufonius	.	.	.	2	.	.	.	0.3
Stellaria longifolia	.	.	.	2	.	.	.	0.3
Ranunculus cymbalaria	.	.	.	2	.	.	.	0.3
Rorippa islandica	.	.	.	2	.	.	.	0.3
Plantago major	.	.	.	2	.	.	.	0.3

$\bar{x}$ Mean.
A Number of species.
a Prominence value (rounded off).
+ Species achieving their highest prominence values by stratum in this community type.

Plate 12. *Salix interior/Typha latifolia* community in the *S. interior/T. latifolia* (Shrub Immature Marsh) Community Type of zone 60 at site #2 in the Lake Athabasca Marsh study area.

Herb-Dwarf Shrub Stratum

This stratum is composed of 20 graminoids, 9 forbs, 4 woody species, and 3 horsetails (Table 21). The mean number of species per community in this stratum is 15. Average stratum cover is 25%, the 4th lowest recorded (Table 2). *Typha latifolia* is most prominent, followed closely by *Eleocharis acicularis* and, to a lesser extent, by *Phalaris arundinacea*, *Carex atherodes*, *Deschampsia caespitosa*, *Carex retrorsa*, *Salix interior*, and *Eleocharis palustris* (Table 21). Total live dwarf-shrub density is 8,300 stems/ha, composed mainly of *S. interior* and *S. lutea* (Table 13).

b. Environment

This CT occurs along the fore-slopes of levees in the LAM study area. The zones are very prone to flooding with an average height of 0.4 m ASWL (range: 0-0.8 m). This CT is very frequently inundated by annual flood-waters for up to three months during the growing season.

The neutral (7.1) to moderately alkaline (7.9) soils of this CT are all Gleyed Regosols. The soils have high calcium carbonate and available nitrogen values; medium sodium and available potassium values; and low conductivity, sulphate, and available phosphorus values. Sedimentation rates are high. Deposited sediments are exclusively loams. Silt content is most variable with the

sand fraction dominant and averaging 46%. The average S/C ratio is 2.6 (range: 1.9-3.1). The average profile organic content is low. The topography is depressional to strongly sloping. Soils have a mean field soil moisture content of 35% (range: 33-40%). These values equal FC and are *ca.* 4x PWP. These relationships indicate a moderate soil moisture surplus possibly resulting from the influence of the hydrologic regime. Soil samples taken during the 1971 growing season indicate a maximal influence of the hydrologic regime in spring. The narrow range of soil moisture values in the zones probably reflects uniformity in soil texture. Poorly drained conditions prevail in this CT.

c. Integration

This CT occupies the hygric to mesic range of the moisture gradient. *Eleocharis acicularis*, *Phalaris arundinacea*, *Limosella aquatica*, *Senecio congestus*, and *Triglochin maritima* in the herb-dwarf shrub stratum achieve their highest mean PV's here (Table 21, App. 9). These species are categorized as "subhygrophytic".

These species achieve the highest prominence in this CT because of their superior competitive ability in tolerating specific durations of flood waters and variable drawdown periods. Observations by Brink (1954) indicate that *Phalaris arundinacea* is not seriously affected by prolonged flooding. Experiments performed by McKenzie

(1951) revealed that *Phalaris* seeds, seedlings, and mature plants have different flood duration tolerances of 35-56, 35-49, and more than 49 days respectively. Besides high tolerances to flooding, this and other species have life cycles that are phenologically well-adapted to the normal times and durations of flooding and to the subsequent drawdown along distributary channels. A typical example is *Senecio congestus* which produces wind-disseminated seeds that germinate to form rosettes on newly exposed alluvial sediments in the fall which over winter, resume growth, and tolerate flooding while maturing in May and June. Flowering occurs in late June just after the normal flood peak and the seeds are dispersed in early July when waters are receding, and mudflats and shorelines are becoming exposed (Baldwin 1950, Martin 1953, Kadlec 1962, Harris & Marshall 1963). The typical *Senecio* cycle occurred during 1969-70 when the flood lasted 11 days in late June, 1970 and was not injurious to most plants in this CT. The cycle was not successfully completed in 1970-71 when the flood was higher and lasted 24 days from late June to mid-July, 1971; it probably failed again in 1971-72 when summer water levels were 60-90 cm higher than in 1971. *Senecio congestus* and other prominent species in this CT appear to require a moist, soft, medium-textured substrate in order for their seeds to establish. Interactions of the hydrologic and edaphic regimes provide adverse

conditions for the establishment of many species which can not tolerate very frequent flooding and sedimentation.

Typha latifolia usually precedes or crowds in upon *Salix interior* in this CT which has no *Carex* cover of consequence and is exposed to wave action and channel currents. This CT has a particularly tenuous habitat and seems less stable than the last four CT's. This conclusion is supported by the youth of its woody species and the absence of dead individuals. The adverse hydrologic regime prevents formation of the extensive shrub and herb-dwarf shrub strata. The prominent species of this CT are light-demanding and quite tolerant of periodic but, perhaps, not severly oxygen-deficient soil conditions. The environmental severity of this CT is reflected in its relatively low species diversity and vitality.

Vegetational and environmental characteristics suggest that this CT is an unstable stage controlled and maintained by allogenic factors. This distinct CT is similar to the Shore Association of Raup (1935), Emergent and Mud Flat Habitat Types of Townsend (1973b), and the Immature Fen CT of Dirschl *et al.* (1974).

9. *Salix interior/Equisetum arvense* (Levee Herb) CT
Zone # 1, 3-7, 12-21, 23-25 (Fig. 2)

a. Vegetation

This CT is composed of 19 communities located in exposed areas generally between Algal Aquatic and Levee Shrub CT's. It is restricted to, but very common throughout, the RC study area (Fig. 3). It is most similar to the Swale Shrub, followed by Shrub Immature Marsh and Levee Shrub CT's. Mean similarity among its communities is 51%, the 4th lowest recorded (Table 1). No subtypes are recognized in this CT (Table 22).

The mean number of vascular species per community is 11, the 4th lowest recorded (Table 2). Five herb species are exclusive to this CT and eight in the herb-dwarf shrub stratum have their highest mean PV's here (Table 22, App. 9). This type has a poorly developed shrub stratum and a moderately developed herb-dwarf shrub stratum (Pl. 13). This CT has the 4th lowest detritus cover; the same woody detritus cover as in the Wet Meadow CT; the same moss cover as in the Shrub Immature Marsh CT; and no liverworts, mushrooms, lichens, and trees (Table 2). The total biomass averages 740 kg/ha with shrubs (46%) and forbs (41%) contributing most of the weight (Table 4). Representative age is 4 years, the 4th youngest CT (Table 12).

Table 22. Species prominence in the ***Salix interior/Equisetum arvense*** (Levee Herb) Community Type.

Study Area		Revillon Coupé																			x̄
Site Number		1	3	3	3	3	1	3	3	3	2	3	3	2	2	2	1	1	1	1	
Zone Number		3	25	20	19	18	1	21	23	24	12	16	17	15	13	14	5	4	6	7	
Species Composition																					
Shrub Stratum: A		2	3	3	3	2	3	3	2	2	2	2	2	2	3	2	3	3	3	4	2.6
Salix interior		375[a]	375	375	375	179	30	19	179	179	3	3	78	3	179	155	63	19	23	100	143
S. lutea		.	126	155	375	63	2	126	155	78	3	3	19	19	179	155	19	19	2	200	89
S. bebbiana		.	63	.	179	.	126	.	.	.	.	.	.	.	.	.	.	.	.	.	19
S. pyrifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	3	.	63	.	3.7
S. lasiandra		.	.	63	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	3.4
S. pseudomonticola		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	63	.	2	3.4
Cornus stolonifera		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	63	3.3
Salix petiolaris		3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Herb-Dwarf Shrub Stratum: A		17	14	13	17	9	5	6	9	6	2	3	3	6	7	8	14	16	18	28	10
Equisetum arvense	+	5	200	200	200	375	.	375	200	675	2	200	375	.	19	3	4	4	100	200	165
Salix interior	+	100	23	89	155	78	100	.	63	3	2	3	4	3	19	2	100	100	63	179	57
S. lutea		.	179	100	179	3	.	126	78	2	.	.	19	3	3	4	19	89	23	3	44
S. bebbiana		27	2	30	155	126	27	126	78	2	.	.	.	.	.	.	.	.	.	179	40
Artemisia biennis	+	126	89	27	126	200	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30
Equisetum palustre		2	.	100	.	.	200	2	.	.	.	.	.	3	19	126	2	2	2	2	24
Salix pyrifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	179	30	89	.	16
Rorippa islandica		2	3	78	.	3	2	2	19	2	.	.	.	.	.	4	2	23	155	2	16
Juncus alpinus	+	.	.	.	.	.	.	.	.	.	.	.	.	3	.	237	13	13	.	.	14
Melilotus alba	+	155	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8.2
Potentilla anserina	+	.	155	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8.2
Epilobium angustifolium		.	155	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8.2
Plantago major		2	19	63	2	63	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7.8
Carex retrorsa		.	.	63	.	.	.	19	3	.	.	19	.	.	2	.	3	2	27	2	7.4
Epilobium glandulosum		2	3	63	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	23	5.1
Agropyron trachycaulum	+	.	.	3	4	78	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4.5
Carex sychnocephala		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	63	.	3.5
Picea glauca		.	.	63	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3.5
Populus balsamifera		63	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3.3
Eleocharis palustris		.	.	.	.	.	.	.	.	.	.	.	.	2	3	2	19	.	.	.	1.4
Juncus balticus		19	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.	.	.	2	1.3
J. nodosus		2	.	.	.	.	.	.	19	.	.	.	.	.	.	.	.	.	2	2	1.3
Sparganium angustifolium		.	.	.	.	.	.	.	23	.	.	.	.	.	.	.	.	.	.	.	1.2
Cornus stolonifera		.	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1.2
Potentilla norvegica		2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19	1.1
Puccinellia nuttalliana		2	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.1
Ranunculus macounii		.	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.0
Hordeum jubatum		.	.	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.0
Rumex maritimus		.	2	.	.	2	.	.	.	.	.	.	.	.	.	.	2	2	2	3	0.7
Limosella aquatica		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	2	2	0.5
Carex aquatilis		.	.	.	.	.	.	.	.	.	.	.	.	3	.	3	.	2	.	.	0.4
Ranunculus sceleratus		.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	2	2	0.3
Equisetum hyemale	+	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	0.3
Juncus bufonius		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	0.2
Carex bebbii		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	0.2
Mimulus guttatus	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	0.2
Sphenopholis obtusata		3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Eleocharis acicularis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	0.2
Equisetum fluviatile		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Poa palustris		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Fragaria vesca		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
F. virginiana		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Lathyrus ochroleucus		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Vicia americana		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Mentha arvensis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Erigeron philadelphicus		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Chenopodium leptophyllum	*	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.1
C. capitatum	*	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	0.1
Kochia scoparia	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	0.1
Collomia linearis	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	0.1
Bidens cernua		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	0.1
Alnus tenuifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	0.1
Achillea sibirica		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	0.1

x̄ Mean.
A Number of species.
a Prominence value (rounded off).
+ Species achieving their highest prominence values by stratum in this community type.
* Species by stratum exclusive to this community type.

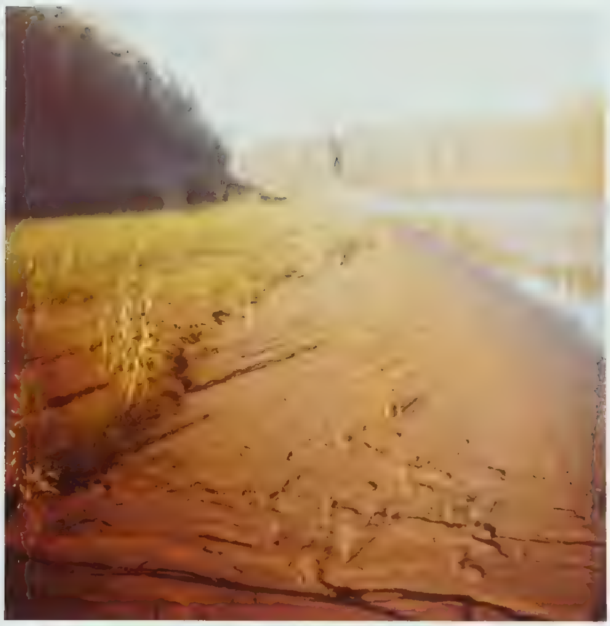


Plate 13. *Salix interior/Equisetum arvense* community of the *S. interior/E. arvense* (Levee Herb) Community Type in the lower section of the Revillon Coupé study area.

Shrub Stratum

Average shrub cover is 27%, the same as the Meadow CT. The mean number of species per community in this stratum is 3, the same as in the Meadow CT (Table 2). *Salix interior* is dominant, followed by *S. lutea* and *S. bebbiana*. The other five species are unimportant in this CT (Table 22). Total live and dead shrub densities are 22,100 and 30 (5th lowest recorded) stems/ha, with *S. interior* providing most of the live and all the dead stems (Table 10). The average height of live individuals is 6 dm (Table 11); the average age of live individuals is 3 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 25 forbs, 16 graminoids, 8 woody species, and 4 horsetails (Table 22). The mean number of species per community in this stratum is 10. Stratum cover averages 43% (Table 2). *Equisetum arvense* is dominant, followed by seedlings of *Salix interior*, *S. lutea*, and *S. bebbiana*, and then by *Artemisia biennis*, *Equisetum palustre*, *Salix pyrifolia*, *Rorippa islandica*, and *Juncus alpinus*. *Mimulus guttatus*, *Chenopodium leptophyllum*, *Chenopodium capitatum*, *Kochia scoparia*, and *Collomia linearis* are exclusive to this CT (Table 22, App. 9). Total live dwarf-shrub density is 20,100 stema/ha with major contributions coming from *S. lutea*, *S. interior*, and *S. bebbiana* (Table 13).

b. Environment

This CT occurs only in the RC study area in a variety of lower riparian zones situated on islands, cut-banks, mudflats, slip-off slopes, and terrace steps. The zones are very prone to flooding and rapidly fluctuating water levels with an average height of 0.7 m ASWL (range: 0-2.2 m). This CT is very frequently inundated by annual flood waters for up to four months during the growing season.

The neutral (7.0) to mildly alkaline (7.8) soils of this CT are all Orthic Regosols. The soils have high sulphate and calcium carbonate values; medium conductivity values; and low sodium and available nitrogen, phosphorus, and potassium values. Sedimentation rates are high and variable. Deposited soil textures are mostly sandy loam followed, to a much lesser extent, by sand and loamy sand. More coarse-textured sediments are deposited here than in the Levee Shrub and Levee Tree CT's. The sand fraction is most variable and dominant, averaging 71% (the highest recorded). The average S/C ratio is 13.6, highest recorded among CT's (range: 5.4-47.5). Average profile organic content is low. Relatively high exposure to wind and radiation, steep slopes, and very high sand content of the soils combine to dessicate the upper solum creating mesic to subxeric surface conditions when water levels recede especially in the higher zones

of this CT. However, the proximity in terms of height and distance to the channel waters prevents the drying of the lower solum allowing subhydric to subhygric conditions to prevail. These same conditions exist in soils of lower, mostly depressional to level zones which may be occasionally classed as hydric during high sustained channel water levels. The average field soil moisture content is 24% (range: 18-32%) and is 1x FC and 5x PWP. These relationships indicate a high soil moisture surplus resulting from the prevailing influence of the hydrologic regime. The extreme variability in soil moisture regime probably reflects the close correspondence to water-level fluctuations. Well-drained conditions predominate when the zones are not inundated.

c. Integration

This CT occupies the mesic to subxeric range of the moisture gradient after flood waters recede. *Equisetum arvense*, *Salix interior*, *Artemisia biennis*, and five other species in the herb-dwarf shrub stratum have their highest mean PV's here (Table 22, App. 9). These species and those exclusive to this CT are tentatively categorized as "subhygrophytic".

During and after spring break-up, moving ice and high-velocity, debris-laden flood waters regularly shear off tops of shrubs, above and below ground sections of susceptible plants and large amounts of sediments from

most zones. Subsequent wave action and rapidly fluctuating water levels further erode sediments and expose root/ rhizome systems at successively lower water levels during spring and summer flood recessions. This action is most noticeable when a reversing current regime develops in the Coupé as Lake Athabasca outflows begin to contest the direction of flow from the Peace River, and during short periods of extreme water-level fluctuations resulting from interactions of appropriate current and wind velocities. In 1970 and 1971, the erosive action was concentrated in lower zones of this CT producing new series of micro-steps. With continued but inconsistent drawdown, as in 1970, many opportunistic and fast growing annuals and biennials quickly invade the newly exposed bare ground producing a phenological series among lower riparian species along these micro-steps (Pl. 13). When local growing seasons are greatly truncated, as in 1971, little or no seed production and poorly developed phenological series occur on late-release zones adjacent to channel waters. During normal drawdown years, the surfaces of upper parts of certain zones, having fine-textured sediments, dry out rapidly producing a hardpan *ca.* 1 cm thick. This hardpan, exhibiting characteristic irregular polygonal patterns, inhibits the establishment and growth of annuals and biennials. The hardpan forms an impenetrable barrier to germinating seedlings as evidenced by numerous

and poorly developed buried plants. However, seedlings did grow in dessication cracks. Thus, riparian species must penetrate through the soft surface during the critical drawdown period before newly exposed sediments become too compact.

Species exclusive to this CT and those achieving their highest prominence here have a distinct advantage by completing their life cycles in complete rhythm with the extremely variable hydrologic conditions. This advantage is accomplished mainly in the characteristic possession of extensive root/rhizome systems which readily produce adventitious roots (*e.g.*, *Salix interior*) or additional rhizomes (*e.g.*, *Equisetum arvense*). The latter species has the highest PV because it can withstand exposure to wind and radiation, prolonged periods of flooding, high rates of sedimentation, and extremely variable soil moisture regimes. In more inhospitable locations, *E. arvense* exhibits a decumbent nature because of higher water velocity and greater sediment abrasion. Species such as *Potentilla anserina* have an equal ability for vegetative and sexual reproduction. During adverse conditions it produces numerous runners giving rise to "separate" individuals which, in turn, produce more runners and individuals. This mode of vegetative reproduction is an effective means of maintaining this species during prolonged flooding periods. These different methods of

rapid vegetative propagation as well as vertical and lateral extension of root systems are extremely efficient adaptations to prolonged floods and substrate instabilities.

Vegetative reproduction is the dominant means of maintaining and increasing the abundance of most species which exhibit very poor ability for sexual reproduction. Some annuals (*e.g.*, *Bidens cernua*) and biennials (*e.g.*, *Senecio congestus*) have life cycles that are phenologically well adapted to normal times and durations of flooding and to subsequent drawdowns (See p. 157). However, the 1971 and 1972 floods caused considerable mortality, reduced vitality and growth, and delayed reproductive phenology not only in these but among many other riparian species. Plants in flower at the onset of the 1971 flood seemed more vulnerable to injury and less able to maintain their preflood status than non-flowering members of the same or other species.

McKenzie (1951) found that *Agropyron trachycaulum* is not seriously affected by prolonged flooding as its seeds, seedlings, and mature plants have different flood duration tolerances of 35-56, 21-35, and 49-63 days respectively. These tolerances help explain this species' occurrence in more exposed and low areas of communities 18-20 which are subjected to most annual floods (Table 22). McKenzie found *Melilotus alba* to be more sensitive to

flooding as its seeds and mature plants have flood tolerances of only 7-14 and 10-14 days respectively. *Melilotus*, occurring in more sheltered and higher areas of community 3, is unaffected by most annual floods (Table 22). Generally, members of the Gramineae appear more tolerant of flooding than those of Leguminosae. The low species richness of this CT tends to support the observation of Ahlgren and Hansen (1957) that flooding and its associated effects are deleterious to the survival and growth of many terrestrial plants.

This CT is considered to have the most unfavourable environment observed in the study region. This rigorous environment contributes to the low species richness, effectively eliminating all species (*e.g.*, shade-demanding and flood-intolerant plants) which can not adjust, especially in their life cycles, to the ever-changing environmental conditions. Each successive flood drastically changes the physical character of essentially all zones in this CT by reducing or eliminating the vertical and horizontal extent of exposed zones while building-up and extending other sheltered downstream zones. Species of this CT appear to be controlled by physical rather than biotic factors.

Vegetational and environmental characteristics suggest that this CT is an unstable stage controlled and maintained by allogenic factors. This distinct CT is

comparable to the Herbaceous Association of Raup (1935), the Mudflat and Low Shrub Habitat Types of Townsend (1973b), and the Low Shrub CT of Dirschl *et al.* (1974).

10. *Alnus tenuifolia/Epilobium angustifolium* (Swale Shrub) CT
Zone # 40, 41, 45 (Fig. 2)

a. Vegetation

This CT is composed of 3 communities located in sheltered areas between Herb Immature Marsh and Levee Shrub CT's. It occurs on a very limited basis and only in the RC study area (Fig. 3). This CT is most similar to the Levee Shrub, followed by Levee Herb and Marsh CT's. Mean similarity among its communities is 64%, the 2nd highest recorded (Table 1). There are no subtypes in this CT (Table 23).

The mean number of vascular species per community is 16 (Table 2). One species in the tree stratum is exclusive to this CT, and two species in the shrub stratum and seven in the herb-dwarf shrub stratum have their highest mean PV's here (Table 23, App. 9). This CT has a very poorly developed tree stratum and moderately developed shrub and herb-dwarf shrub strata (Pl. 14). This CT has the highest liverwort and 2nd highest detritus covers (Table 2). No biomass sampling was conducted here. Representative age of this CT is 27 years (Table 9).

Table 23. Species prominence in the *Alnus tenuifolia/ Epilobium angustifolium* (Swale Shrub) Community Type

Study Area		RC			$\bar{x}$
Site Number		4			
Zone Number		40	41	45	
Species Composition					
Tree Stratum: A		1	.	.	0.3
Salix interior	*	375[a]	.	.	125
Shrub Stratum: A		3	4	5	4.0
Alnus tenuifolia	+	675	179	375	410
Salix interior		200	200	3	134
S. lutea		2	13	89	35
S. pseudomonticola		.	2	89	30
Betula papyrifera	+	.	.	63	21
Herb-Dwarf Shrub Stratum: A		11	16	18	15
Epilobium angustifolium	+	2	179	375	185
Equisetum fluviatile		2	100	200	101
Alnus tenuifolia	+	100	100	78	93
Picea glauca	+	200	30	27	86
Salix bebbiana		.	23	89	37
S. interior		2	100	3	35
Equisetum palustre	+	2	3	89	31
Scutellaria galericulata		.	27	63	30
Salix lutea		2	2	27	10
Equisetum pratense		30	.	.	10
Potentilla norvegica	+	.	3	23	8.7
Mentha arvensis		19	3	.	7.3
Plantago major		.	19	3	7.3
Sphenopholis obtusata	+	.	19	.	6.3
Populus balsamifera		.	19	.	6.3
Rorippa islandica		.	19	.	6.3
Equisetum arvense		2	.	3	1.7
Ranunculus cymbalaria	+	3	.	.	1.0
Typha latifolia		.	3	.	1.0
Calamagrostis canadensis		.	.	3	1.0
Epilobium glandulosum		.	.	3	1.0
Lysimachia thyrsiflora		.	.	3	1.0
Agropyron trachycaulum		.	.	2	0.7
Achillea millefolium		.	.	2	0.7
Aster ciliolatus		.	.	2	0.7

RC Revillon Coupé study area.
$\bar{x}$ Mean.
A Number of species.
a Prominence value (rounded off).
* Species in its tree form exclusive to this community type.
\+ Species achieving their highest prominence values by stratum in this community type.

Plate 14. *Salix interior/Epilobium angustifolium* community in the *Alnus tenuifolia/E. angustifolium* (Swale Shrub) Community Type of zone 41 at site #4 in the Revillon Coupé study area.

Tree Stratum

Average cover of this stratum is 12%. The mean number of species per community in this stratum is 0.3 (Table 2). *Salix interior* is the only species in this stratum (Table 23) and reaches a larger size class (sapling) here than in any other CT. Total live and dead sapling densities are 1,200 and 750 stems/ha (Table 7). Average heights of live and dead individuals are 6.8 and 5.5 m (Table 8). The average age of live individuals is 27 years (Table 9).

Shrub Stratum

Average shrub cover is 53%. The mean number of species per community in this stratum is 4 (Table 2). *Alnus tenuifolia* is dominant followed, to a much lesser extent, by *Salix interior*. The other three species are unimportant here (Table 23). Total live and dead shrub densities are 89,000 and 4,000 stems/ha. *Alnus tenuifolia* and *S. interior* provide most of the live density, with the latter species contributing most of the dead density (Table 10). Stratum height averages 12 dm (Table 11). The average age for this stratum is 5 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 11 forbs, 6 woody species, 4 graminoids, and 4 horsetails (Table 23). The

mean number of species per community in this stratum is 15. Average stratum cover is 48% (Table 2). The tall forb *Epilobium angustifolium* is most prominent, followed by *Equisetum fluviatile*, *Alnus tenuifolia*, and *Picea glauca* and, to a much lesser extent, by *Salix bebbiana*, *S. interior*, *Equisetum palustre*, and *Scutellaria galericulata* (Table 23). Total live dwarf-shrub density is 33,300 stems/ha, the major components being seedlings of *P. glauca* and *A. tenuifolia*, but other woody species are also important (Table 13).

b. Environment

This CT occurs along swale slopes in a point-bar channel behind a log-jam at site #4 in the RC study area. The zones are prone to frequent flooding with an average height of 0.2 m ASWL (range: 0-0.5 m). The zones may be wholly or partially inundated by periodic flood waters that breach or over-top the log-jam at one end of the channel or by annual waters that over-top the levee at the other end. This CT may be inundated for up to three months after floods during the growing season.

The poorly developed and mildly alkaline (7.6) soils of this CT are probably Regosols. The soils have high conductivity, sulphate, calcium carbonate, and available nitrogen values; medium sodium values; and low available phosphorus and potassium values. Sedimentation

rates are low to moderate. Soil textures are loam and sandy loam. Sand and silt contents are quite variable, and sand is the dominant fraction, averaging 50%. The average S/C ratio is 4.4 (range: 3.5-4.8). Average profile organic content is low. The topography ranges from very gently to moderately sloping zones. The average field soil moisture content is 29% (range: 16-38%), slightly lower than FC and *ca.* 4x PWP. These relationships indicate a moderate soil moisture surplus resulting from the prevailing influence of the climatic regime. However, soil samples taken during the 1971 growing season indicate a great influence of the hydrologic regime in spring. The wide variability in the soil moisture regime probably reflects differences in zonal conditions. The zones in this CT are imperfectly to well-drained.

c. Integration

This CT occupies the subhygric to submesic range of the moisture gradient. ***Alnus tenuifolia*** and ***Betula papyrifera*** in the shrub stratum, and ***Epilobium angustifolium***, ***A. tenuifolia***, and five other species in the herb-dwarf shrub stratum have their highest mean PV's in this CT (Table 23, App. 9). These species and ***Salix interior*** (in the tree stratum) are categorized as "submesophytic".

These species are adapted to inorganic substrates having medium- and coarse-textured sediments and rela-

tively stable water-levels that have a net drawdown during the growing season. The combination of declining influence from the hydrologic regime, moderate physiographic controls, and good soil drainage and moisture status permits *Salix interior* to reach sapling stage only in this CT. These factors also aid the development of *Alnus tenuifolia*, *Betula papyrifera*, and *Picea glauca* as viable species components. The total absence of any ice action is perhaps the single major factor contributing to the abundant and excellent growth of these species.

This unique CT is a result of the log-jam blocking the point-bar channel. It has ameliorated hydrologic, climatic, and edaphic regimes which eliminate or reduce the abundance of many Herb Immature Marsh and Levee Herb species, while favouring more mesophytic Upland Forest species. This CT is still controlled mainly by physical factors, but biotic factors are becoming more important. Removal of the physiographic control may drastically alter communities of this CT, perhaps forcing a regression to the Levee Herb CT.

Vegetational and environmental characteristics indicate that this CT is derived from an unstable stage controlled by allogenic factors some of which have been ameliorated. This relatively distinct CT is similar to the Shrub Association of Raup (1935), the Low Shrub Habitat Type of Townsend (1973b), and the Low Shrub CT of

Dirschl *et al.* (1974).

11. *Alnus tenuifolia/Cornus stolonifera* (Levee Shrub) CT

Zone # 2, 8, 9, 26-29, 34, 35, 39, 46, 47 (Fig. 2)

a. Vegetation

This CT is composed of 12 communities located in relatively exposed areas generally between Levee Herb and Levee Tree, and between Swale Shrub and Levee Tree CT's. It is restricted to, but common throughout, the RC study area (Fig. 3). It is most similar to Swale Shrub, followed by Levee Tree and Levee Herb CT's. Mean similarity among its communities is 53% (Table 1). There are no subtypes in this CT (Table 24).

The mean number of vascular species per community is 12 (Table 2). One herb species is exclusive to this CT, and two species in the shrub stratum and one in the herb-dwarf shrub stratum have their highest mean PV's here (Table 24, App. 9). This type has a poorly developed tree stratum, a highly developed shrub stratum, and a very poorly developed herb-dwarf shrub stratum (Pl. 15). This CT has the 2nd highest woody detritus cover (Table 2). Total understory biomass averages 1,300 kg/ha with shrubs contributing 88% (Table 4). Representative age is 39 years, the 6th oldest CT (Table 19).

Table 24. Species prominence in the ***Alnus tenuifolia/Cornus stolonifera*** (Levee Shrub) Community Type.

Study Area		Revillon Coupé												$\bar{x}$
Site Number		1	3	4	4	4	4	1	1	3	3	3	4	
Zone Number		2	26	34	39	47	46	9	8	27	28	29	35	
Species Composition														
Tree Stratum: A		.	.	.	3	.	.	.	.	.	.	3	.	0.5
Salix bebbiana		.	.	.	675[a]	.	.	.	.	.	.	126	.	67
Alnus tenuifolia		.	.	.	375	.	.	.	.	.	.	237	.	51
Populus balsamifera		.	.	.	19	.	.	.	.	.	.	427	.	37
Shrub Stratum: A		4	6	5	5	4	6	5	6	6	5	6	5	5.2
Alnus tenuifolia		155	179	19	13	850	850	675	290	675	375	155	675	409
Salix interior	+	200	335	335	3	100	200	19	375	126	126	63	.	157
S. lutea		126	126	27	89	.	13	.	335	126	155	155	126	106
S. bebbiana		155	375	3	.	.	13	63	179	.	.	.	.	66
Populus balsamifera		.	126	13	13	2	13	78	.	126	126	89	89	56
Cornus stolonifera		.	.	.	13	30	2	78	19	19	155	179	13	42
Salix lasiandra	+	.	63	.	.	.	.	.	63	.	.	.	63	16
Rosa acicularis		.	.	.	.	.	.	.	.	.	.	155	.	13
Salix pseudomonticola		.	.	.	.	.	.	.	.	2	.	.	.	0.2
Herb-Dwarf Shrub Stratum: A		16	18	10	12	13	17	11	12	7	4	4	7	11
Cornus stolonifera		3	27	.	.	3	3	63	2	3	89	126	89	34
Alnus tenuifolia		3	19	.	.	179	23	63	2	4	2	2	19	26
Salix lutea		.	23	200	3	.	2	63	23	.	.	.	.	26
Equisetum pratense		2	.	2	5	3	100	89	3	.	.	.	30	20
E. palustre		89	.	27	2	5	23	.	78	.	.	.	.	19
Salix bebbiana		27	78	.	.	19	19	63	3	.	.	3	.	18
S. interior		3	89	23	3	3	27	3	19	2	2	.	.	14
Equisetum arvense		19	100	.	2	.	.	23	23	3	.	.	.	14
Picea glauca		.	.	.	2	100	30	3	.	.	.	.	3	12
Epilobium glandulosum		.	.	.	.	.	89	.	3	.	.	.	.	7.7
Rubus pubescens		.	.	.	.	63	23	.	.	.	.	.	.	7.2
Agropyron trachycaulum		2	3	.	3	.	3	3	23	.	.	.	.	3.1
Plantago major		13	19	2	.	.	.	.	.	.	.	.	3	3.1
Equisetum fluviatile		.	.	.	.	.	30	.	.	.	.	.	.	2.5
Fragaria vesca		.	.	.	.	2	19	3	2	.	.	.	.	2.2
Rubus strigosus		.	.	.	.	2	23	.	.	.	.	.	.	2.1
Juncus balticus	+	.	.	23	.	.	.	.	.	.	.	.	.	1.9
Mentha arvensis		3	.	.	19	.	.	.	.	.	.	.	.	1.8
Carex retrorsa		.	.	19	.	.	.	.	.	.	.	.	.	1.6
Populus balsamifera		.	2	2	.	.	2	2	.	2	3	2	2	1.4
Ribes oxyacanthoides		.	.	.	.	.	13	.	.	.	.	.	.	1.1
Erigeron philadelphicus		3	3	.	2	.	.	.	.	.	.	.	3	0.9
Artemisia biennis		2	2	3	2	.	.	.	.	.	.	.	.	0.8
Aster ciliolatus		2	2	.	.	.	.	.	.	2	.	.	.	0.5
Poa palustris		3	.	3	.	.	.	.	.	.	.	.	.	0.5
Potentilla norvegica		.	3	.	.	.	3	.	.	.	.	.	.	0.5
Rorippa islandica		.	2	.	3	.	.	.	.	.	.	.	.	0.4
Aster puniceus		.	3	.	.	.	.	.	.	.	.	.	.	0.2
Cinna latifolia		.	.	.	3	.	.	.	.	.	.	.	.	0.2
Achillea sibirica		.	.	.	.	.	.	.	3	.	.	.	.	0.2
Calamagrostis canadensis		2	.	.	.	.	.	.	.	.	.	.	.	0.2
Melilotus alba		2	.	.	.	.	.	.	.	.	.	.	.	0.2
Sisyrinchium montanum	■	.	2	.	.	.	.	.	.	.	.	.	.	0.2
Salix lasiandra		.	2	.	.	.	.	.	.	.	.	.	.	0.2
Achillea millefolium		.	2	.	.	.	.	.	.	.	.	.	.	0.2
Agrostis scabra		.	.	.	.	2	.	.	.	.	.	.	.	0.2
Poa pratensis		.	.	.	.	2	.	.	.	.	.	.	.	0.2
Carex bebbii		.	.	.	.	2	.	.	.	.	.	.	.	0.2
Solidago lepida		.	.	.	.	.	.	.	.	2	.	.	.	0.2

$\bar{x}$ Mean.
A Number of species.
a Prominence value (rounded off).
+ Species achieving their highest prominence values by stratum in this community type.
■ Species by stratum exclusive to this community type.

Plate 15. *Salix bebbiana/Equisetum arvense* community in the *Alnus tenuifolia/Cornus stolonifera* (Levee Shrub) Community Type of zone 26 at site #3 of the Revillon Coupé study area.

Tree Stratum

Average cover of this stratum is 23%. The mean number of species per community in this stratum is 0.5 (Table 2). *Salix bebbiana* is most prominent, followed closely by *Alnus tenuifolia* and *Populus balsamifera* (Table 24). Total basal areas are 3.9 and 0.6 m^2/ha for live and dead trees. The three species contribute about equally to live basal area, while *A. tenuifolia* is the major contributor to dead basal area (Table 16). Total live and dead tree densities are 220 and 7 stems/ha, with *S. bebbiana* being the major contributor to both (Table 17). Total live and dead sapling densities are 450 and 330 stems/ha, with *S. bebbiana* and *A. tenuifolia* major contributors to both (Table 7). Average tree height for live is 9.3 m and for dead individuals 6.1 m (Table 18). Average sapling height is 6.8 m for live and 6.0 m for dead individuals (Table 8). Average age of live trees is 32 years (Table 19), of saplings 31 years (Table 9).

Shrub Stratum

Average shrub cover is 78%, the highest recorded. The mean number of species per community in this stratum is 5, the 4th highest recorded (Table 2). *Alnus tenuifolia* is dominant, followed distantly by *Salix interior*, *S. lutea*, *S. bebbiana*, *Populus balsamifera*, and *Cornus stolonifera*. The other three species have PV's less than

20 (Table 24). Total live and dead shrub densities are 73,600 and 2,200 stems/ha, with *A. tenuifolia* the main contributor to both (Table 10). This stratum has an average height of 12 dm (Table 11), and an average live age of 7 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 16 forbs, 10 woody species, 9 graminoids, and 4 horsetails (Table 24). The mean number of species per community in this stratum is 11. Average cover of this stratum is 20%, the 3rd lowest recorded (Table 2). *Cornus stolonifera* is most prominent, followed very closely by *Alnus tenuifolia*, *Salix lutea*, *Equisetum pratense*, *E. palustre*, *Salix bebbiana*, *S. interior*, and *Equisetum arvense*. Only *Sisyrinchium montanum* is exclusive to this CT (Table 24, App. 9). Total live dwarf-shrub density is 22,800 stems/ha with major contributions from *C. stolonifera* and *S. interior*, and lesser amounts from *A. tenuifolia* and *S. bebbiana* (Table 13).

b. Environment

This CT occurs predominantly on mid-levee locations of islands, cut-banks, terrace steps, and point-bar channels of the RC study area. The zones have an average height of 2.1 m ASWL (range: 0-4.2 m), and are less prone to flooding than the Levee Herb CT. This CT is frequently

to infrequently flooded for up to two months during the growing season.

The neutral (7.0) to mildly alkaline (7.8) soils of this CT are all Orthic Regosols. The soils have high calcium carbonate values; medium conductivity, sulphate, and available phosphorus and potassium values; and low sodium and available nitrogen values. Sedimentation rates are moderate to high. Soil textures are sandy loam followed, to a much lesser extent, by loam. More medium-textured sediments are deposited in this CT than very coarse sediments which have settled out in the Levee Herb CT. Sand and silt contents are most variable, and sand is the dominant fraction averaging 57% (2nd highest recorded). The S/C ratio is 5.7, the 3rd highest recorded (range: 3.1-8.8). Average profile organic content is low. The topography ranges from gently to strongly sloping zones. The rapid drainage of the upper solum in the higher zones of this CT create mesic to subxeric surface conditions; less rapidly drained zones have subhygric to mesic conditions. The average field soil moisture content is 23%, the lowest recorded (range: 15-37%), slightly lower than FC and *ca.* 4x PWP. These relationships indicate a moderate soil moisture surplus resulting from the prevailing influence of the climatic regime. However, soil samples taken during 1971 growing season indicate a great influence of the hydrologic regime in spring. Imperfectly to rapidly drained conditions occur in this

CT, with well-drained situations predominating.

c. Integration

This CT occupies the subhygric to submesic range of the moisture gradient. *Salix interior* and *S. lasiandra* in the shrub stratum and *Juncus balticus* in the herb-dwarf shrub stratum have their highest mean PV's here (Table 24, App. 9). These species and *Sisyrinchium montanum* are categorized as "submesophytic".

These species achieve the highest prominence in this CT because of a distinct advantage in tolerating both annually non-destructive and periodically devastating floods which contribute greatly to the poorly developed herb and tree strata. The tree stratum and a highly developed shrub stratum effectively reduce wind and water velocity and radiation promoting increases in relative humidity and smaller temperature fluctuations. Slightly ameliorated hydrologic, climatic, and edaphic regimes eliminate or reduce the abundance of many Levee Herb species while increasing the number of more mesic Upland Forest species. The environmental severity of this CT is reflected in the relatively poor diversity and vitality of its species.

During high spring floods, ice action and high velocity flood-waters cause considerable damage in this CT. Besides scarring, shearing, and uprooting shrub

stems, the ice, water, and sediment cause substantial deformation of stems, especially of *Salix interior*, by bending them in a downstream position. Other species, *e.g. Alnus tenuifolia*, can endure these periodically devastating effects only where protected by *S. interior* stems. During the 1972 flood, much sediment and detritus were removed from most zones and re-deposited in downstream zones. *Salix interior* was seriously affected while *A. tenuifolia* on higher and more inland zones was not. In more steeply sloping zones of this CT, severe and repeated ice scouring and water action in 1972 further undercut the slopes forming cut-banks with ledges fully exposing numerous water-trained roots, mainly of *Populus balsamifera*. The vegetation's inability to stabilize the underlying slopes eventually permitted the ledge and its plants to fall into the channel. The resulting drowned trees form "deadheads" that encourage downstream build-up of debris and sediment essential to the formation or extension of Levee Herb zones. Ice and water action exert intermittent but firm control of this CT, restricting species occurrences and abundances while transforming this levee habitat.

Vegetational and environmental characteristics indicate that this CT is a relatively unstable stage controlled and held in check by allogenic factors. This relatively distinct CT is comparable to the Shrub . . .

Association of Raup (1935), the Low Shrub Habitat Type of Townsend (1973b), and the Low Shrub CT of Dirschl *et al.* (1974).

12. *Populus balsamifera/Cornus stolonifera/Equisetum pratense* (Levee Tree) CT
Zone # 10, 11, 30-32, 36, 37, 48 (Fig. 2)

a. Vegetation

This CT is composed of 8 communities generally located in sheltered areas between Levee Shrub and Upland Forest CT's. It occurs on a limited basis and only in the RC study area (Fig. 3). It is most similar to the Upland Forest, followed by Levee Shrub and Wet Lowland Forest CT's. Mean similarity among its communities is 60%, the 4th highest recorded (Table 1). There are no subtypes in this CT (Table 25).

The mean number of vascular species per community is 11, the same as in the Levee Herb CT (Table 2). No species are exclusive to this CT but two species in the tree stratum, three in the shrub stratum, and five in the herb-dwarf shrub stratum have their highest mean PV's here (Table 25, App. 9). This type has a very highly developed tree stratum, a highly developed shrub stratum, and a poorly developed herb-dwarf shrub stratum (Pl. 16). It has the 3rd highest detritus and woody detritus covers, and no liverworts (Table 2). Total understory biomass averages 388 kg/ha (2nd lowest recorded) with shrubs

Table 25. Species prominence in the *Populus balsamifera/Cornus stolonifera/ Equisetum pratense* (Levee Tree) Community Type.

Study Area		Revillon Coupé								x̄
Site Number		4	4	3	3	3	1	1	4	
Zone Number		48	37	32	30	31	10	11	36	
Species Composition										
Tree Stratum: A		3	4	4	3	3	2	3	3	3.1
Populus balsamifera	+	45[a]	89	335	850	155	760	850	675	470
Alnus tenuifolia	+	850	375	335	155	850	375	89	290	415
Picea glauca		.	.	45	63	63	.	13	89	34
Salix bebbiana		155	63	.	.	.	.	.	.	27
Betula papyrifera		.	63	126	.	.	.	.	.	24
Shrub Stratum: A		4	8	6	3	5	4	6	4	5.0
Cornus stolonifera	+	19	3	200	675	375	375	675	179	313
Rosa acicularis		.	2	335	200	155	126	375	179	172
Alnus tenuifolia		335	78	78	.	126	89	63	45	102
Populus balsamifera	+	200	179	.	.	126	13	23	.	68
Viburnum edule		.	.	.	.	.	.	179	126	38
Ribes triste	+	2	3	155	.	.	.	.	.	20
Salix bebbiana		.	3	13	13	126	.	.	.	19
Rubus strigosus		.	126	.	.	.	.	.	.	16
Shepherdia canadensis		.	.	89	.	.	.	.	.	11
Ribes oxyacanthoides		.	.	.	.	.	.	13	.	1.6
R. hudsonianum		.	2	.	.	.	.	.	.	0.2
Herb-Dwarf Shrub Stratum: A		9	8	10	6	8	5	7	8	7.6
Equisetum pratense	+	30	100	100	30	200	200	200	100	120
Rosa acicularis		.	.	200	179	63	3	89	19	69
Fragaria vesca		2	155	78	89	63	.	.	.	48
Cornus stolonifera		2	3	63	126	126	3	3	19	43
Alnus tenuifolia		.	.	63	.	63	3	.	.	16
Aralia nudicaulis	+	.	.	126	.	.	.	.	.	16
Mertensia paniculata		.	.	.	.	.	.	126	.	16
Populus balsamifera	+	63	.	.	.	.	.	3	2	8.5
Galium triflorum	+	.	.	63	.	.	.	.	.	7.9
Pyrola asarifolia		.	.	.	.	63	.	.	.	7.9
Shepherdia canadensis		.	.	13	.	.	.	.	.	1.6
Agrostis scabra		2	.	2	2	2	2	.	.	1.2
Cinna latifolia	+	2	4	.	.	.	.	.	3	1.1
Picea glauca		2	.	.	.	.	.	3	.	0.6
Poa pratensis		.	2	.	.	2	.	.	.	0.5
Pyrola secunda		.	3	.	.	.	.	.	.	0.4
Scutellaria galericulata		.	3	.	.	.	.	.	.	0.4
Poa palustris		.	.	.	.	.	.	.	3	0.4
Viburnum edule		.	.	.	.	.	.	.	3	0.4
Sphenopholis obtusata		2	.	.	.	.	.	.	.	0.2
Rubus strigosus		2	.	.	.	.	.	.	.	0.2
Arenaria lateriflora		.	2	.	.	.	.	.	.	0.2
Ribes triste		.	.	2	.	.	.	.	.	0.2
Salix bebbiana		.	.	.	2	.	.	.	.	0.2
Epilobium angustifolium		.	.	.	.	.	.	2	.	0.2
Calamagrostis canadensis		.	.	.	.	.	.	.	2	0.2

x̄ Mean.
A Number of Species.
[a] Prominence Value (rounded off).
\+ Species achieving their highest prominence values by stratum in this community type.

Plate 16. *Populus balsamifera/Cornus stolonifera/ Equisetum pratense* community of the *P. balsamifera/C. stolonifera/E. pratense* (Levee Tree) Community Type in the lower section of the Revillon Coupé study area.

(53%) and forbs (38%) contributing the most (Table 4). Representative age is 137 years, the 2nd oldest CT (Table 19).

Tree Stratum

Average cover of this stratum is 89%, the highest recorded. The mean number of species per community in this stratum is 3, the 3rd highest recorded (Table 2). *Populus balsamifera* is the most prominent of five species, followed closely by *Alnus tenuifolia* (Table 25). Total live and dead basal areas are 28.2 and 3.5 m^2/ha, the former being the highest here. *Populus balsamifera* is the main contributor to both readings (Table 16). Total live and dead tree densities are 1,300 and 80 stems/ha, with *P. balsamifera* and *A. tenuifolia* the main contributors to both (Table 17). Total live and dead sapling densities are 1,300 and 630 stems/ha with *A. tenuifolia* the main contributor to both (Table 7). Average height of live trees is 9.8 m and of dead trees 9.4 m (tallest recorded; Table 18). Average height of live saplings is 5.5 m and of dead saplings 4.7 m (Table 8). Average age of live trees is 85 years (Table 19) with saplings being 28 years (Table 9).

Shrub Stratum

Average shrub cover is 68%, the 2nd highest recorded. The mean number of species per community in this stratum is 5, the same as in the Levee Shrub CT (Table 2). *Cornus stolonifera* is dominant, followed by *Rosa acicularis*, *Alnus tenuifolia*, and *Populus balsamifera*. The other seven species have PV's less than 40 (Table 25). Total live and dead shrub densities are 41,900 and 5,000 stems/ha with *C. stolonifera* being the main contributor to both (Table 10). This stratum has an average height of 10 dm (Table 11). The average age of live individuals is 8 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 10 woody species, 9 forbs, 6 graminoids, and 1 horsetail (Table 25). The mean number of species per community in this stratum is 8, the 3rd lowest recorded. Stratum cover averages 36% (Table 2). *Equisetum pratense* is dominant, followed by *Rosa acicularis*, *Fragaria vesca*, and *Cornus stolonifera* (Table 25). Total live dwarf-shrub density is 16,800 stems/ha; the major contributors being *R. acicularis* and *C. stolonifera*, *A. tenuifolia*, and *Populus balsamifera* (Table 13).

b. Environment

This CT occurs on slopes, crests, and swales of higher levees in the RC study area. The zones have an average height of 3.2 m ASWL (range: 2.3-4.2 m), and are less prone to flooding than those in the Levee Shrub CT. This CT is rarely inundated but, when flooded, the waters may last up to half a month during the growing season.

The neutral (7.0) to mildly alkaline (7.8) soils of this CT are generally Cumulic Regosols. The soils have high calcium carbonate values; medium available potassium values; and low sodium, conductivity, sulphate, and available nitrogen and phosphorus values. Sedimentation is negligible, at present. Soil textures are mostly sandy loam and then loam. Because of their greater height and distance from the channel, the zones have more medium-textured sediments; all coarse and all very coarse sediments settle out in the Levee Herb and Shrub CT's. The sand content is most variable and is the dominant fraction, averaging 56%. The average S/C ratio is 5.8, the 2nd highest recorded (range: 2.7-7.9). Average profile organic content is low. The topography ranges from very gently to moderately sloping zones. The mean field soil moisture content of 16% is the lowest recorded among CT's (range: 12-19%); slightly less than FC and *ca.* 3x PWP. These relationships indicate a moderate soil moisture surplus with occasional deficits modulated by the climatic

regime. This conclusion is substantiated by soil samples taken during the 1971 growing season. Inter-zonal variations in the soil moisture levels are small, probably due to the uniformity in soil texture. Well-drained and moderately well-drained conditions prevail in this CT.

c. Integration

This CT occupies the mesic and submesic segments of the moisture gradient. *Populus balsamifera* and *Alnus tenuifolia* in the tree stratum; *Cornus stolonifera* and *P. balsamifera* in the shrub stratum; and *Equisetum pratense* and *Aralia mudicaulis* in the herb-dwarf shrub stratum achieve, among other species, their highest mean PV's here (Table 25, App. 9). These species are categorized as "mesophytic".

These species achieve the highest prominence in this CT because of their superior competitive ability on zones with rarely occurring floods of short duration and minimal depth. The lower swale zone (#31) of this CT shows considerable evidence of flood damage, and may be water-logged for most of the summer due to inadequate internal and external drainages. Such swale zones are imperfectly drained and may have poor soil aeration which reduces root respiration of mesophytic species to a critically low level. Thus, *Populus balsamifera* which requires a moderate sand content for proper aeration and root respiration is drastically affected by prolonged

flooding (Lacate 1965, Gill 1971). This effect is shown by the relatively low PV's of this species in swales *cf.* ridges where the soil is warmer, drier, and better aerated (Table 25). No individuals exhibited peripheral stem-rot symptoms of impending death from flooding, but many had varying degrees of heart rot typical of over-maturity and community senescence. This situation may indicate marginal conditions for *P. balsamifera* and more intense competition from *Alnus tenuifolia* in swale zones. These two species attain their highest PV's in this CT because of an inability to tolerate annual flooding and concomitant sedimentation. *Alnus* prefers moist soil but can not endure floods of long duration; it has a poor ability to grow adventitious roots. Ridge and swale zones with a high prominence of *A. tenuifolia* have slightly higher available nitrogen contents in their soils compared to adjacent zones of other CT's (App. 3), possibly resulting from N-fixing bacterial root nodules in *Alnus* (Tarrant 1968, Odum 1971). Crocker and Major (1955) found that nitrogen fixation in *Alnus* increases total nitrogen content from 10 to nearly 300 gm/m^2 in a forest soil profile for a 92-year period at Glacier Bay, Alaska. The incorporation of nitrogen into soils of communities in this CT may be important for succeeding communities.

The interior climate of this CT is highly ameliorated compared to previous levee CT's; the increased shade

from tree and shrub canopies has reduced the range of fluctuating temperatures, increased relative humidity and reduced wind velocity. Herb species such as *Equisetum pratense* and *Aralia nudicaulis* are well-adapted to this ameliorated situation. The high shade and lack of annual flooding effectively eliminate light- and flood-tolerant species of preceding levee CT's. On the other hand, shade-tolerant but flood-intolerant species of succeeding CT's are not present in this periodically flooded CT. The result is a low herb-dwarf shrub species diversity in this CT.

Vegetational and environmental characteristics suggest that this CT is a relatively stable seral stage controlled by polygenic factors. This distinct CT is comparable to the Tree Association of Raup (1935), the Deciduous Tree Habitat Type of Townsend (1973b), and the Deciduous Forest CT of Dirschl *et al.* (1974).

13. *Picea glauca/Rosa acicularis/Viburnum edule*
(Upland Forest) CT
Zone # 33, 38, 49, 84, 93, 102, 111, 119, 120, 129, 130, 137, 146, 155 (Fig. 2)

a. Vegetation

This CT is composed of 14 communities and is common in sheltered locations of all study areas except LAM. In the absence of flooding, it tends to succeed Levee Tree, Fen, Moist Lowland Forest, Wet Lowland Forest, and Bog CT's (Fig. 3). This type is most similar to Wet Lowland Forest and Levee Tree CT's. Mean similarity among its

communities is 54% (Table 1). No subtypes are recognized in this CT (Table 26).

The mean number of vascular species per community is 27, the 3rd highest recorded (Table 2). Three species in the shrub stratum and 10 in the herb-dwarf shrub stratum are exclusive to this CT, and two species in the tree stratum, four in the shrub stratum, and 22 in the herb-dwarf shrub stratum have their highest mean PV's here (Table 26, App. 9). This type has highly developed tree and shrub strata and a moderately developed herb-dwarf shrub stratum (Pl. 17). This CT includes the tallest communities recorded, and has the highest lichen cover, the 4th highest detritus cover, and no liverworts (Table 2). Total understory biomass averages 890 kg/ha with shrubs (50%) and forbs (33%) contributing most of the weight (Table 4). Representative age is 145 years, the oldest recorded CT (Table 19).

Tree Stratum

Average cover of this stratum is 78%, the 3rd highest recorded. The mean number of species per community in this stratum is 4, the 2nd highest recorded (Table 2). *Picea glauca* is dominant followed by *Populus balsamifera*, *P. tremuloides*, *Salix bebbiana* and, to a much lesser extent, by *Betula papyrifera*, *Alnus tenuifolia*, *Salix arbusculoides*, and *S. scouleriana* (Table 26). Total basal areas are 26.0 and 4.2 m^2/ha for live and dead trees,

Table 26. Species prominence in the *Picea glauca/Rosa acicularis/Viburnum edule* (Upland Forest) Community Type.

Study Area		Revillon Coupé			Nuphar Lake			Chilaway Snye			Egg Lake					$\bar{x}$
Site Number		4	4	3	1	2	3	2	1	3	3	1	2	2	3	
Zone Number		38	49	33	137	146	155	93	84	102	130	111	120	119	129	
Species Composition																
Tree Stratum: A		5	5	3	4	3	3	5	5	4	5	5	4	2	1	3.9
Picea glauca		89[a]	45	523	375	604	375	850	63	89	375	45	.	.	.	245
Populus balsamifera		290	375	.	.	.	.	.	.	89	155	675	675	3	.	162
P. tremuloides	+	.	.	.	375	63	675	23	335	375	.	89	.	.	.	138
Salix bebbiana		19	155	.	.	.	.	.	155	89	375	.	.	375	675	132
Betula papyrifera	+	126	89	290	13	.	.	23	335	.	179	13	179	.	.	89
Alnus tenuifolia		325	63	13	13	13	.	13	13	.	89	.	126	.	.	48
Salix arbusculoides		.	.	.	.	.	126	.	.	.	.	200	63	.	.	28
S. scouleriana		.	.	.	.	.	.	19	.	.	.	.	.	.	.	1.4
Shrub Stratum: A		5	9	9	9	6	6	6	10	9	7	6	5	7	6	7.1
Rosa acicularis	+	375	179	335	126	63	179	63	179	200	179	179	375	63	200	192
Viburnum edule	+	126	200	179	200	13	63	3	200	45	.	.	375	89	.	107
Cornus stolonifera		19	375	63	2	.	13	.	13	2	78	126	290	126	155	90
Shepherdia canadensis		.	.	63	126	179	375	19	126	.	2	.	.	.	.	64
Salix bebbiana		.	126	.	.	2	.	.	155	4	155	.	.	126	63	45
Amelanchier alnifolia	*	.	.	19	45	.	.	.	427	19	.	.	.	.	.	36
Picea glauca		.	.	63	126	89	155	3	3	.	.	63	.	.	.	36
Rubus strigosus	+	63	63	2	.	2	.	.	13	63	.	.	.	45	63	22
Alnus tenuifolia		155	.	63	89	.	.	.	.	.	.	2	.	.	.	22
Ribes triste		.	.	.	.	.	.	.	.	.	.	.	.	63	179	17
R. oxyacanthoides	+	.	2	63	2	.	.	.	.	19	3	.	63	63	2	16
Populus balsamifera		.	179	.	.	.	.	.	.	.	2	19	.	.	.	14
Betula papyrifera		.	.	.	.	.	.	.	.	126	63	.	.	.	.	14
Salix arbusculoides		.	.	.	.	.	.	.	.	.	.	126	63	.	.	14
Populus tremuloides		.	.	.	126	.	.	3	19	.	.	.	.	.	.	11
Symphoricarpos albus	*	.	.	.	.	.	63	.	3	.	.	.	.	.	.	4.7
Ribes lacustre	*	.	2	.	.	.	.	.	.	2	.	.	.	.	.	0.3
R. hudsonianum		.	2	.	.	.	.	.	.	.	.	.	.	.	.	0.1
Salix scouleriana		.	.	.	.	.	.	2	.	.	.	.	.	.	.	0.1
Herb-Dwarf Shrub Stratum: A		14	17	23	20	23	24	26	23	18	32	22	26	28	29	23
Viburnum edule	+	19	100	78	200	126	155	2	155	2	19	2	675	63	.	114
Rosa acicularis	+	200	4	23	200	200	200	2	63	30	4	126	100	2	3	83
Equisetum pratense		200	30	30	.	2	2	2	3	3	100	200	100	375	100	82
Pyrola asarifolia	+	4	200	100	2	78	63	30	200	78	3	.	19	.	3	56
Cornus canadensis	+	.	155	200	100	23	78	3	13	2	100	2	100	.	2	56
Linnaea borealis	+	.	19	89	179	100	3	3	179	.	3	.	.	.	.	41
Ribes oxyacanthoides	+	.	126	23	2	63	63	.	2	3	78	2	63	63	78	40
Rubus pubescens	+	2	.	.	3	.	.	2	.	.	.	.	2	335	19	26
Mertensia paniculata		.	63	23	.	63	63	.	.	.	78	.	63	.	.	25
Pyrola secunda	+	2	63	19	.	19	2	2	89	.	2	.	19	.	89	22
Calamagrostis canadensis		.	.	.	.	.	.	.	.	.	3	30	.	2	200	17
Shepherdia canadensis	+	.	.	4	2	179	23	.	.	.	2	.	.	.	.	15
Galium boreale	*	.	.	19	23	3	23	3	19	100	.	.	19	.	.	15
Fragaria vesca		3	78	89	3	.	3	2	3	3	3	.	19	2	.	15
Epilobium angustifolium		.	.	78	2	19	63	2	2	3	2	2	2	2	30	15
Rubus strigosus	+	2	63	.	.	23	.	4	19	2	27	2	19	2	23	13
Arctostaphylos uva-ursi		.	.	.	179	.	.	2	.	.	.	.	.	.	.	13
Maianthemum canadense	+	.	.	19	78	.	2	2	63	3	2	2	2	.	.	12
Mitella nuda	+	3	63	23	19	19	.	.	.	.	19	.	2	.	.	11
Anemone canadensis	+	.	.	.	.	.	.	.	.	.	63	.	.	2	63	9.1
Cornus stolonifera		19	3	.	.	2	2	2	2	2	2	63	19	.	3	8.5
Poa palustris		.	.	.	.	.	3	.	.	3	3	2	.	100	2	8.1
Rubus acaulis		.	.	.	.	19	89	.	.	.	.	.	.	.	.	7.7
Picea glauca		2	2	23	2	63	2	3	3	.	2	2	.	.	2	7.6
Lathyrus ochroleucus	+	.	.	.	23	13	19	.	23	4	.	2	19	2	.	7.5
Aralia nudicaulis		.	.	78	.	.	.	2	3	.	2	2	2	2	.	6.5
Scutellaria galericulata		.	.	.	.	.	.	.	.	.	2	2	.	63	3	5.0
Galium triflorum		.	.	.	.	.	.	.	.	.	19	3	.	2	45	4.9
Geum macrophyllum	+	.	.	.	.	.	.	.	.	.	.	.	.	63	3	4.7
Actaea rubra	+	.	.	19	.	.	.	.	.	.	.	.	19	13	2	3.8
Viola nephrophila	*	.	.	30	.	.	.	.	.	.	.	.	2	.	.	2.3
Fragaria virginiana	+	.	.	23	2	2	2	2	.	.	.	.	.	.	.	2.2
Stellaria longifolia		.	.	.	.	.	.	.	.	.	2	3	.	2	23	2.1
Vicia americana		3	4	19	.	2	.	.	.	.	.	.	.	.	.	2.0
Achillea millefolium	+	.	.	19	2	.	2	.	2	2	.	.	.	.	.	1.9
Alnus tenuifolia		.	.	19	.	.	.	.	.	.	.	.	2	2	2	1.8
Salix pseudomonticola	+	.	.	.	.	.	23	.	.	.	.	.	.	.	.	1.6
S. bebbiana		.	19	.	.	2	.	.	.	.	.	.	.	.	.	1.5
Agrostis scabra		.	.	.	.	.	2	4	2	2	2	2	.	2	2	1.3
Solidago lepida	+	.	2	.	.	.	.	.	2	.	2	2	2	.	.	0.7
Achillea sibirica	+	.	.	.	.	.	.	.	.	.	3	.	.	3	3	0.6
Potentilla norvegica		.	.	.	.	.	2	.	.	.	2	.	.	2	2	0.6
Amelanchier alnifolia	*	.	.	.	2	.	.	.	3	3	.	.	.	.	.	0.6
Pyrola virens	*	3	.	.	.	2	.	2	.	.	.	.	.	.	.	0.5
Geocaulon lividum		.	.	.	.	4	.	3	.	.	.	.	.	.	.	0.5
Aster ciliolatus		.	.	.	.	.	.	.	2	.	.	2	2	.	.	0.4
Cinna latifolia		.	.	.	.	.	.	.	.	.	2	2	2	.	.	0.4
Populus balsamifera		.	.	.	.	.	.	3	.	.	2	.	.	.	.	0.4
Ribes triste	+	.	.	.	.	.	.	.	.	.	2	.	.	.	2	0.3
R. hudsonianum		.	.	.	.	.	.	.	.	.	.	2	2	.	.	0.3
Arenaria lateriflora		.	.	.	.	.	.	.	.	.	.	.	.	2	2	0.3
Erigeron philadelphicus		.	.	.	.	.	.	.	.	.	.	.	.	2	2	0.3
Poa interior	*	.	.	.	.	.	.	3	.	.	.	.	.	.	.	0.2
Campanula rotundifolia	*	.	.	.	.	.	.	3	.	.	.	.	.	.	.	0.2
Symphoricarpos albus	*	.	.	.	.	.	.	.	.	3	.	.	.	.	.	0.2
Sium suave		.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Viola adunca		.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Mentha arvensis		.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Artemisia biennis		2	.	.	.	.	.	.	.	.	.	.	.	.	.	0.1
Elymus innovatus		.	.	.	2	.	.	.	.	.	.	.	.	.	.	0.1
Polypodium vulgare	*	.	.	.	.	.	.	2	.	.	.	.	.	.	.	0.1
Saxifraga tricuspidata	*	.	.	.	.	.	.	2	.	.	.	.	.	.	.	0.1
Populus tremuloides		.	.	.	.	.	.	.	2	.	.	.	.	.	.	0.1
Betula papyrifera		.	.	.	.	.	.	.	.	.	2	.	.	.	.	0.1
Thalictrum venulosum	*	.	.	.	.	.	.	.	.	.	.	.	2	.	.	0.1
Rumex mexicanus		.	.	.	.	.	.	.	.	.	.	.	.	2	.	0.1
Cicuta douglasii		.	.	.	.	.	.	.	.	.	.	.	.	2	.	0.1
Heracleum lanatum		.	.	.	.	.	.	.	.	.	.	.	.	2	.	0.1
Petasites vitifolius		.	.	.	.	.	.	.	.	.	.	.	.	2	.	0.1

$\bar{x}$ Mean.
A Number of species.
a Prominence value (rounded off).
+ Species achieving their highest prominence values by stratum in this community type.
* Species by stratum exclusive to this community type.

Plate 17. *Picea glauca/Shepherdia canadensis/Rosa acicularis* community in the *P. glauca/R. acicularis/Viburnum edule* (Upland Forest) Community Type of zone 146 at site #2 in the Nuphar Lake study area.

the latter being the highest recorded. *Populus balsamifera* and *P. glauca* contribute most to live basal area, and *S. bebbiana* most of the dead basal area (Table 16). Total live and dead tree densities are 1,600 and 250 stems/ha, both peaking in this CT. *Populus tremuloides* and *S. arbusculoides* are the major contributors to live and dead tree densities, respectively (Table 17). Total live and dead sapling densities are 2,000 and 1,100 (highest recorded) stems/ha. *Populus tremuloides* and *S. bebbiana* are major contributors to live and dead sapling densities, respectively (Table 7). Average live tree height is 11.2 m (tallest recorded) and for dead individuals 7.5 m (Table 18). Average live sapling height is 6.2 m; for dead it is 4.8 m (Table 8). Average age of live trees is 78 years (Table 19), of saplings 43 years (Table 9).

Shrub Stratum

Average shrub cover is 63%, the 5th highest recorded. The mean number of species per community in this stratum is 7, the 2nd highest recorded (Table 2). *Rosa acicularis* is most prominent of 19 species followed by *Viburnum edule*, *Cornus stolonifera* and, to a much lesser extent, by *Shepherdia canadensis*, *Salix bebbiana*, *Amelanchier alnifolia*, and *Picea glauca* (Table 26). *Amelanchier alnifolia*, *Symphoricarpos albus*, and *Ribes lacustre* are exclusive to this CT (Table 26, App. 9). Total live and

dead shrub densities are 43,400 and 8,900 stems/ha with *R. acicularis*, *V. edule*, *S. canadensis*, and *C. stolonifera* being the major contributors to both densities (Table 10). The average height of live individuals is 11 dm (Table 11); the average age of live individuals is 12 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 43 forbs (highest recorded), 18 woody species, 6 graminoids, 1 horsetail, and 1 fern (Table 26). The mean number of species per community in this stratum is 23, the 3rd highest recorded. Average stratum cover is 60% (Table 2). *Viburnum edule* is dominant, followed by *Rosa acicularis* and *Equisetum pratense* and, to a lesser extent, by *Pyrola asarifolia*, *Cornus canadensis*, *Linnaea borealis*, and *Ribes oxyacanthoides*. *Galium boreale*, *Viola nephrophila*, *Amelanchier alnifolia*, and seven other species in this stratum are exclusive to this CT (Table 26, App. 9). Total live dwarf-shrub density is 42,800 stems/ha, the highest recorded, with *V. edule* and *R. acicularis* making the major contributions (Table 13).

b. Environment

This CT occurs on crests and lee slopes of higher levees, and on lower slopes of extensive Precambrian outcrops and isolated knolls in all study areas except LAM.

The zones have an average height of 3.3 m ASWL (range: 1.2-5.8 m), and consequently are rarely if ever flooded. The lowermost zones occur in restricted and isolated drainage systems that have relatively stable water levels.

Soil types of this CT are variable with Orthic Gray Luvisols predominating over Cumulic Orthic Gray Luvisols, Fera Gleysols, and Orthic Gleysols. Soil pH ranges from medium acid (5.6) to moderately alkaline (8.3). The soils have high available phosphorus values; medium sodium, conductivity, sulphate, calcium carbonate, and available potassium values; and low available nitrogen values. No sedimentation takes place, at present, in the zones. Soil textures are mostly sandy loam, followed by sandy clay loam, loam, and clay. Clay content is quite variable, and sand is the dominant fraction averaging 54%, the same as in the Fen CT. The average S/C ratio is 4.4 (range: 1.0-7.2). Average profile organic content is medium. The topography ranges from nearly level to strongly rolling zones. Soils have a mean field moisture content of 24%, the same as in the Levee Herb CT (range: 9-48%), slightly lower than FC and *ca.* 3x PWP. These relationships indicate a moderate soil moisture surplus, with occasional deficits altered by the climatic regime. Soil samples taken during the 1971 growing season showed a wide variation in soil moisture, probably due to variations in rainfall intensity and run-off. Well-drained and,

to a much lesser extent, moderately well-drained conditions occur in this CT.

c. Integration

This CT occupies the mesic and submesic segments of the moisture gradient. *Populus tremuloides* in the tree stratum, *Rosa acicularis* in the shrub stratum, and *Viburnum edule* in the herb-dwarf shrub stratum achieve, among other species, their highest mean PV's here (Table 26, App. 9). These species and those exclusive to this CT are categorized as "mesophytic".

Mesophytic species show excellent vitality and achieve high PV's in this CT because of their superior competitive abilities in the absence of flooding and sedimentation. Though this CT has an ameliorated environment, variations in canopy cover and community structure give rise to large differences in controlling factors. In open areas created by windfall, light-tolerant species (*e.g.*, *Betula papyrifera* and *Fragaria virginiana*) are dominant. Under a dense canopy, shade-tolerant species (*e.g.*, *Rubus pubescens*, *Anemone canadensis*, and *Mitella nuda*) are more prominent.

Vegetational and environmental characteristics suggest that this CT is a stable stage in succession controlled by autogenic factors. This distinct CT is comparable to the Tree Association of Raup (1935), the Floodplain Type of the *Picea glauca* Association of Moss (1955), the

Forest Association of Horton (1965), the Coniferous Tree Habitat Type of Townsend (1973b), and the Coniferous Forest CT of Dirschl *et al.* (1974).

14. *Salix bebbiana/S. bebbiana/Equisetum pratense* (Moist Lowland Forest) CT
Zone # 82, 83, 91, 92, 101 (Fig. 2)

a. Vegetation

This CT is composed of five communities located in sheltered areas between Meadow and Upland Forest and between Fen and Upland Forest CT's. It occurs on a limited basis and only in the CS study area (Fig. 3). This type is most similar to the Fen, followed by Wet Lowland Forest, Levee Tree, Meadow, and Upland Forest CT's. Mean similarity among its communities is 38%, the 3rd lowest recorded (Table 1). There are no subtypes in this CT (Table 27).

The mean number of vascular species per community is 14 (Table 2). No species are exclusive to this CT but two species in the tree stratum, four in the shrub stratum, and one in the herb-dwarf shrub stratum have their highest mean PV's here (Table 27, App. 9). This type has a moderately developed tree stratum, poorly developed shrub stratum, and very poorly developed herb-dwarf shrub stratum (Pl. 18). This CT has the highest woody detritus cover, the same lichen cover as in the Upland Forest CT, and no liverworts (Table 2). The total understory biomass averages 840 kg/ha with shrubs (51%) and graminoids (48%)

Table 27. Species prominence in the *Salix bebbiana/S. bebbiana/Equisetum pratense* (Moist Lowland Forest) Community Type.

Study Area		Chilaway Snye					$\bar{x}$
Site Number		1	1	2	3	2	
Zone Number		83	82	91	101	92	
Species Composition							
Tree Stratum: A		1	1	1	2	4	1.8
Salix bebbiana	+	375[a]	.	375	850	.	320
Populus tremuloides		.	.	.	63	375	88
Salix arbusculoides		.	290	.	.	.	58
S. scouleriana	+	.	.	.	.	179	36
Picea glauca		.	.	.	.	89	18
Populus balsamifera		.	.	.	.	63	13
Shrub Stratum: A		2	4	4	1	3	2.8
Salix bebbiana		126	155	200	78	.	112
S. arbusculoides	+	335	126	.	.	.	92
S. serissima	+	.	375	.	.	.	75
Populus tremuloides	+	.	.	63	.	100	33
Picea glauca		.	.	3	.	2	1.0
Salix scouleriana	+	.	2	.	.	2	0.8
Betula papyrifera		.	.	3	.	.	0.6
Herb-Dwarf Shrub Stratum: A		11	17	12	11	9	12
Equisetum pratense		30	23	100	30	78	52
Carex atherodes		19	155	3	.	.	35
Picea glauca		.	.	100	.	30	26
Calamagrostis canadensis		.	23	27	4	2	11
Poa pratensis		23	.	.	.	.	4.6
Ranunculus macounii		19	3	.	.	.	4.4
Polygonum amphibium		19	2	.	.	.	4.2
Arenaria lateriflora	+	.	2	19	.	.	4.2
Betula papyrifera		19	.	.	.	.	3.8
Sphenopholis obtusata		.	19	.	.	.	3.8
Agrostis scabra		2	2	2	2	2	2.0
Poa palustris		3	3	.	3	.	1.8
Alnus tenuifolia		.	2	2	2	2	1.6
Galium trifidum		.	3	3	.	.	1.2
Pyrola asarifolia		.	.	.	3	3	1.2
Potentilla norvegica		3	.	.	.	2	1.0
Mentha arvensis		.	3	.	2	.	1.0
Erigeron philadelphicus		.	2	2	.	.	0.8
Salix bebbiana		.	.	2	2	.	0.8
Geum macrophyllum		.	.	2	2	.	0.8
Scutellaria galericulata		.	3	.	.	.	0.6
Sium suave		.	.	3	.	.	0.6
Lathyrus ochroleucus		.	.	.	3	.	0.6
Populus tremuloides		.	.	.	.	3	0.6
Cornus stolonifera		2	.	.	.	.	0.4
Solidago lepida		2	.	.	.	.	0.4
Stellaria longifolia		.	2	.	.	.	0.4
Geum allepicum		.	2	.	.	.	0.4
Aster puniceus		.	2	.	.	.	0.4
A. ciliolatus		.	.	.	2	.	0.4
Epilobium angustifolium		.	.	.	.	2	0.4

$\bar{x}$ Mean.
A Number of species.
[a] Prominence value (rounded off).
+ Species achieving their highest prominence values by stratum in this community type.

Plate 18. *Salix bebbiana/S. bebbiana/Equisetum pratense* community in the *S. bebbiana/S. bebbiana/E. pratense* (Moist Lowland Forest) Community Type of zone 101 at site #3 in the Chilaway Snye study area.

contributing essentially all the weight (Table 4). Representative age is 73 years, the 5th oldest CT (Table 19).

Tree Stratum

Average cover of this stratum is 56%, the 4th highest recorded. The mean number of species per community in this stratum is 2 (Table 2). *Salix bebbiana* is dominant, followed to a much lesser extent by *Populus tremuloides*. The other four species are unimportant in this CT (Table 27). Total basal areas are 11.2 and 1.3 m^2/ha for live and dead trees. *Populus tremuloides* and *S. bebbiana* contribute most to live basal area with the latter species providing most of the dead basal area (Table 16). Total live and dead trees densities are 770 and 16 stems/ha. *Populus tremuloides* and *S. bebbiana* provide most of the live density while *P. balsamifera* is the sole contributor to dead density (Table 17). Total live and dead sapling densities are 5,600 and 930 stems/ha with the former being the highest recorded. *Salix bebbiana* is the main contributor to both densities (Table 7). The average tree height for live is 9.6 m and for dead individuals 6.6 m (Table 18). The average sapling height is 5.5 m for live and 5.0 m for dead individuals (Table 8). Average age for live trees is 48 years (Table 19) with saplings being 22 years (Table 9).

Shrub Stratum

Average shrub cover is 40%. The mean number of species per community in this stratum is 3, the same as in the Meadow CT (Table 2). *Salix bebbiana* is dominant followed, to a lesser extent, by *S. arbusculoides* and *S. serissima*. The other four species are unimportant in this stratum (Table 27). Total live and dead shrub densities are 12,400 and 5,400 stems/ha, with *S. bebbiana* being the main contributor to both (Table 10). Stratum height averages 16 dm (Table 11). The average age for this stratum is 12 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 18 forbs, 6 woody species, 6 graminoids, and 1 horsetail (Table 27). The mean number of species per community in this stratum is 12. Average cover of this stratum is 18%, the 2nd lowest recorded (Table 2). *Equisetum pratense* is most prominent followed, to a lesser extent, by *Carex atherodes* and *Picea glauca* (Table 27). Total live dwarf-shrub density is 8,800 stems/ha with *P. glauca* and *Alnus tenuifolia* being major contributors (Table 13).

b. Environment

This CT occurs along bases of Precambrian knolls in the CS study area. These zones are generally not flooded with an average height of 1.1 m ASWL (range: 0.6-

1.5 m). This CT is infrequently inundated but when flooded the waters may remain for about one month during the growing season.

The strongly acid (5.2) to neutral (7.1) soils of this CT are all Orthic Gleysols. The soils have medium sodium and available phosphorus and potassium values; and low conductivity, sulphate, calcium carbonate, and available nitrogen values. Sedimentation is negligible at present, but may increase with changes in the hydrologic regime. Deposited soil textures are mostly sandy clay loam and sandy clay, followed by clay. Because of the greater height and distance from the channel, more medium-textured sediments have been deposited in these zones during floods which mutually affect this CT and preceding zones of other CT's in this study area. Clay content is quite variable, and the sand fraction is dominant, averaging 51%. The S/C ratio is 1.4 (range: 1.0-1.8). Average profile organic content is low. The topography ranges from depressional to gently sloping zones. The mean field soil moisture content is 35% (range: 21-63%), *ca.* 1x FC and 2x PWP. These relationships indicate a moderate soil moisture surplus resulting from the prevailing influence of the climatic regime. This conclusion is substantiated by soil samples taken during the 1971 growing season. Small inter-zonal variations in the soil moisture levels are probably due to the uniformity in

soil texture. Moderately well-drained conditions prevail in this CT.

c. Integration

This CT occupies the mesic and submesic segments of the moisture gradient. No species are exclusive to this CT but *Salix bebbiana* in the tree stratum, *S. arbusculoides* in the shrub stratum, and *Arenaria laterifolia* in the herb-dwarf shrub stratum have, among other species, their highest mean PV's here (Table 27, App. 9). These species are categorized as "submesophytic".

These species achieve the highest prominence in this CT because of a lack of annual flooding and sedimentation. However, periodic floods have probably contributed to the low species diversity and sparse development in the herb-dwarf shrub and shrub strata. Species in the tree stratum appear unaffected as the periodic floods are of insufficient duration. Generally the above species prefer moderately well-drained zones having medium-textured sediments. This CT has a more ameliorated environment than preceding lowland CT's in the CS study area. The high shade and lack of appreciable periodic flooding effectively reduce the abundances of more light- and flood-tolerant meadow and fen species. On the other hand, shade-tolerant but flood-intolerant species of the succeeding CT's are not present in this CT. The result is a low herb-dwarf shrub diversity in this CT.

Vegetational and environmental characteristics suggest that this CT is a relatively stable stage controlled by polygenic factors. This indistinct CT is comparable to the Tree Association of Raup (1935), the Deciduous Tree Habitat Type of Townsend (1973b), and the Deciduous Forest CT of Dirschl *et al.* (1974).

15. *Picea glauca/Alnus tenuifolia/Geocaulon lividum* (Wet Lowland Forest) CT
Zone # 145, 153, 154 (Fig. 2)

a. Vegetation

This CT is composed of three communities located in sheltered areas between Bog and Upland Forest CT's. It occurs on a very limited basis, and only in the NL study area (Fig. 3). It is most similar to the Upland Forest, followed by Levee Tree and Moist Lowland Forest CT's. Its communities have a mean similarity of 54% (Table 1). There are no subtypes in this CT (Table 28).

The mean number of vascular species per community is 34, the highest recorded (Table 2). Three herb species are exclusive to this CT, and two species in the tree stratum, four in the shrub stratum, and 19 in the herb-dwarf shrub stratum have their highest mean PV's here (Table 28, App. 9). This type has a very highly developed tree stratum, and highly developed shrub and herb-dwarf shrub strata (Pl. 19). This CT has the 2nd highest moss cover and no liverworts (Table 2). No biomass sampling was conducted in this CT. Representative

Table 28. Species prominence in the *Picea glauca/Alnus tenuifolia/Geocaulon lividum* (Wet Lowland Forest) Community Type.

Study Area		Nuphar Lake			$\bar{x}$
Site Number		3	3	2	
Zone Number		153	154	145	
Species Composition					
Tree Stratum: A		4	5	6	5.0
Picea glauca	+	179[a]	335	335	283
Alnus tenuifolia		126	335	375	279
Salix arbusculoides	+	155	126	179	153
Populus balsamifera		78	155	89	107
P. tremuloides		.	.	126	42
Betula papyrifera		.	13	2	5.0
Shrub Stratum: A		6	11	5	7.3
Alnus tenuifolia		200	126	375	234
Picea glauca	+	126	155	375	219
Salix bebbiana		375	200	.	192
Shepherdia canadensis	+	.	335	.	112
Salix myrtillifolia	+	.	.	179	60
S. arbusculoides		126	.	2	43
Populus balsamifera		.	23	.	7.7
Ribes hudsonianum	+	13	2	.	5.0
Salix barklayi (?)		.	2	13	5.0
Rosa acicularis		.	3	.	1.0
Salix serissima		2	.	.	0.7
S. glauca		.	2	.	0.7
Ribes oxyacanthoides		.	2	.	0.7
Rubus strigosus		.	2	.	0.7
Herb-Dwarf Shrub Stratum: A		26	34	31	30
Geocaulon lividum	+	19	179	19	72
Fragaria vesca	+	3	19	179	67
Cornus stolonifera	+	.	.	179	60
Arctostaphylos uva-ursi	+	.	155	3	53
Salix bebbiana	+	126	13	.	46
Mertensia paniculata	+	.	63	63	42
Linnaea borealis		3	23	89	38
Picea glauca		2	3	100	35
Calamagrostis canadensis		.	2	100	34
Salix barklayi (?)	+	.	13	78	30
Calamagrostis inexpansa	+	89	.	.	30
Pyrola asarifolia		78	3	4	28
Ribes oxyacanthoides		.	63	19	27
Carex aquatilis		78	.	.	26
Epilobium palustre	+	78	.	.	26
Equisetum scirpoides	+	19	27	30	25
Rubus acaulis	+	63	4	.	22
Rosa acicularis		.	2	63	22
Betula glandulosa	+	63	.	.	21
Viburnum edule		.	.	63	21
Pyrola secunda		23	2	23	16
Alnus tenuifolia		30	3	4	12
Mitella nuda		19	3	4	8.7
Ranunculus gmelinii		23	.	3	8.7
Poa palustris		19	2	2	7.7
Equisetum fluviatile		23	.	.	7.7
Salix pyrifolia		.	23	.	7.7
Cornus canadensis		.	.	23	7.7
Poa pratensis	+	19	.	.	6.3
Galium trifidum		19	.	.	6.3
Betula papyrifera	+	.	13	.	4.3
Equisetum pratense		3	3	3	3.0
Potentilla norvegica		.	2	4	2.0
Equisetum sylvaticum	+	.	3	3	2.0
Ribes hudsonianum	+	2	3	.	1.7
Shepherdia canadensis		.	2	3	1.7
Agrostis scabra		.	2	2	1.3
Carex canescens		3	.	.	1.0
C. retrorsa		3	.	.	1.0
Sium suave		3	.	.	1.0
Carex concinna	*	.	3	.	1.0
Parnassia palustris	+	.	3	.	1.0
Petasites palmatus	*	.	3	.	1.0
P. vitifolius		.	3	.	1.0
Smilacina trifolia		.	.	3	1.0
Salix myrtillifolia		.	.	3	1.0
Viola adunca	+	.	.	3	1.0
Achillea millefolium		.	.	3	1.0
Oxycoccus microcarpus		2	.	.	0.7
Arenaria lateriflora		.	2	.	0.7
Rubus strigosus		.	2	.	0.7
Aster ciliolatus		.	2	.	0.7
Petasites frigidus	*	.	2	.	0.7
Elymus innovatus	+	.	.	2	0.7
Lathyrus ochroleucus		.	.	2	0.7

$\bar{x}$ Mean.
A Number of species.
a Prominence value (rounded off).
\+ Species achieving their highest prominence values by stratum in this community type.
* Species by stratum exclusive to this community type.

Plate 19. *Alnus tenuifolia/A. tenuifolia-Picea glauca/ Cornus stolonifera-Fragaria vesca* community in the *P. glauca/A. tenuifolia/Geocaulon lividum* (Wet Lowland Forest) Community Type of zone 145 at site #2 in the Nuphar Lake study area.

age is 83 years, the 3rd oldest CT (Table 19).

Tree Stratum

Average tree cover is 89%, the same as in the Levee Tree CT. The mean number of species per community in this stratum is 5, the highest recorded (Table 2). *Picea glauca* and *Alnus tenuifolia* are dominant. The other four species have PV's less than 200 in this stratum (Table 28). Total basal areas are 4.2 and 1.3 m^2/ha for live and dead individuals, with the main contributions to both coming from *P. glauca*, *Populus balsamifera*, and *Salix arbusculoides* (Table 16). Average live and dead tree densities are 270 and 27 stems/ha, with *P. glauca* the main contributor to live, and *P. balsamifera* the sole contributor to dead density (Table 17). Total live and dead sapling densities are 2,200 and 1,000 stems/ha. *Picea glauca*, *A. tenuifolia*, and *S. arbusculoides* provide most of the live, while the latter two species contribute most of the dead density (Table 7). Average tree height is 7.4 m for live, and 6.8 m for dead individuals (Table 18). Average sapling height is 6.5 m for live and 5.1 m for dead individuals (Table 8). The average age of live trees is 54 years (Table 19), of saplings 20 years (Table 9).

Shrub Stratum

Average shrub cover is 68%, the same as in the Levee Tree CT. The mean number of species per community in this stratum is 7, the same as in the Upland Forest CT (Table 2). *Alnus tenuifolia* is most prominent, followed by *Picea glauca* and *Salix bebbiana* and, to a lesser extent, by *Shepherdia canadensis*. The other 10 species have PV's Less than 100 (Table 28). Total live and dead shrub densities are 35,000 and 22,500 stems/ha, with the latter peaking here. *Salix bebbiana* and *A. tenuifolia* are the main contributors to both densities (Table 10). This stratum has an average height of 13 dm (Table 11), and an average live age of 13 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 25 forbs, 16 woody species, 10 graminoids, and 4 horsetails (Table 28). The mean number of species per community in this stratum is 30, the 2nd highest recorded. Stratum cover averages 73%, the 3rd highest recorded (Table 2). *Geocaulon lividum* is most prominent, followed closely by *Fragaria vesca*, *Cornus stolonifera*, *Arctostaphylos uva-ursi*, and *Salix bebbiana*. Fifteen other species have PV's more than 20 in this stratum. *Carex concinna*, *Petasites palmatus*, and *P. frigidus* are exclusive to this CT (Table 28, App. 9). Total live dwarf-shrub density is 34,700 (3rd highest recorded) stems/ha with *Alnus tenuifolia*, *Picea*

glauca, and *Salix barklayi* (?) the main contributors (Table 13).

b. Environment

This CT occurs along bases of Precambrian outcrops in the NL study area. Its three zones are never flooded, being located in a basin behind continuous, high levees. These zones have an average elevation of 0.5 m ASWL (range: 0.2-1.0 m) and are unaffected by small water-level fluctuations occurring in Nuphar Lake.

The neutral (7.0), mineral soils of this CT are Gleysols. The soils have high sodium values; medium conductivity, and available nitrogen and phosphorus values; and low sulphate, calcium carbonate, and available potassium values. The sediments are mostly sandy clay and then clay in texture. Clay is the dominant fraction (43%: highest recorded), followed very closely by sand (41%) which is quite variable. The average S/C ratio is 1.0 (range: 0.5-1.3), the lowest recorded. Average profile organic content is low. The macrotopography ranges from depressional to steeply sloping zones. Mean field soil moisture content is 43%, the 5th highest recorded (range: 26-65%), slightly less than FC and *ca*. 2x PWP. There is a moderate soil moisture surplus, resulting from the climatic regime. Poorly drained and imperfectly drained conditions prevail in this CT.

c. Integration

This CT occupies the hygric to mesic range of the moisture gradient. Species exclusive to this CT and those with the highest prominence here (Table 28, App. 9) are categorized as "subhygrophytic". These species attain their highest prominence in this CT primarily because of their superior competitive abilities in the absence of flooding and sedimentation in poorly drained and relatively wet sites with thick accumulations of organic matter overlying fine-textured sediments. These conditions permit very well-developed strata which produce deep shade, high relative humidity, and small air temperature fluctuations. This CT has a more ameliorated environment than the Bog CT, which eliminates or reduces the abundance of many light- and wet-tolerant bog species and favours growth of upland species. The hummocky microtopography contributes to the highest species diversity in the study region being recorded in this CT.

Vegetational and environmental characteristics suggest that this CT is a stable stage in succession controlled by autogenic factors. This distinct CT is comparable to the Tree Association of Raup (1935), the Deciduous Tree and Coniferous Habitat Types of Townsend (1973b), and the Deciduous Forest and Coniferous Forest CT's of Dirschl *et al.* (1974).

16. *Myrica gale/M. gale* (Bog) CT
Zone # 132-136, 139-144, 148-152 (Fig. 2)

a. Vegetation

This CT is composed of 16 communities located in sheltered areas between Vascular Aquatic and Wet Lowland Forest or Upland Forest CT's. It is very common in and restricted to the NL study area (Fig. 3). This type is most similar to the Wet Lowland Forest CT. Mean similarity among its communities is 54% (Table 1).

This CT has three subtypes. The *Calla palustris* ST is an immature hummock phase composed of four communities (132, 135, 136, 139: Table 29) representing a transition between meadow and other bog communities. This ST is characterized by subhydric conditions, numerous meadow species, and an abundance of hypnic mosses compared to other ST's. It is quite distinct with low similarities to the second (44%) and third (40%) ST's. It is comparable to the initial stages of the *Drepanocladus-Carex* Bog Series of the *Larix laricina* Association of Moss (1953a,b).

The *Larix laricina/L. laricina/Ledum groenlandicum* ST is a mature hummock phase composed of nine communities (133, 134, 140-142, 148-151: Table 29) representing the typical bog stage in this CT. This ST is characterized by hygric conditions, true bog species, and numerous well-developed *Sphagnum* hummocks. Distinct species align-

Table 29. Species prominence in the *Myrica gale/M. gale* (Bog) Community Type.

Study Area		Nuphar Lake																x̄
Site Number		2	1	1	1	1	1	2	2	3	3	3	3	2	2	3	2	
Zone Number		139	132	135	136	133	134	140	141	148	149	150	151	142	143	152	144	
Subtype		A	A	A	A	B	B	B	B	B	B	B	B	B	C	C	C	
Species Composition																		
Tree Stratum: D		.	.	.	2	2	1	2	1	.	1	.	1	1	.	.	2	0.8
Larix laricina	-*	.	.	.	.	200[a]	78	63	19	.	78	.	13	63	.	.	.	32
Picea mariana	-*	.	.	.	.	179	.	179	.	.	.	.	.	.	.	.	.	22
Salix arbusculoides		.	.	.	237	.	.	.	.	.	.	.	.	.	.	.	45	18
Picea glauca		.	.	.	126	.	.	.	.	.	.	.	.	.	.	.	.	7.9
Alnus tenuifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	63	3.9
Shrub Stratum: D		5	5	3	5	8	8	9	9	7	9	8	11	9	8	8	10	7.6
Myrica gale	-*	155	155	63	126	100	200	200	200	200	375	179	375	335	.	126	.	174
Salix pedicellaris	-*	200	375	155	.	89	19	.	19	675	200	3	63	2	126	.	2	120
Chamaedaphne calyculata	*	375	155	155	.	13	2	19	63	89	2	2	375	155	.	155	.	98
Betula glandulosa	*	200	.	.	.	.	.	2	2	200	155	3	89	155	63	200	126	75
B. pumila	*	63	155	.	.	63	2	13	63	78	155	.	89	.	126	63	63	58
Larix laricina	*	.	.	.	.	100	200	155	179	.	89	78	19	78	.	.	.	56
Ledum groenlandicum	*	.	.	.	.	89	179	200	19	63	89	155	2	19	.	.	.	51
Picea mariana	*	.	.	.	.	63	126	375	126	.	3	63	2	.	.	.	.	47
Alnus tenuifolia		.	.	.	63	.	.	.	.	.	.	.	.	.	.	63	375	31
Salix myrtillifolia		.	2	.	.	.	.	2	2	2	2	2	2	2	13	2	335	23
S. pyrifolia		.	.	.	.	.	.	19	.	.	.	.	45	2	126	126	.	20
S. serissima		.	.	.	2	.	.	.	.	.	.	.	2	2	126	126	.	16
S. barklayi (?)	+	.	.	.	126	.	.	.	.	.	.	.	.	.	45	.	45	14
Andromeda polifolia	*	.	.	.	.	23	63	.	.	.	.	.	.	.	45	.	45	11
Picea glauca		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	63	3.9
Salix scouleriana		.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	0.1
S. bebbiana		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	0.1
S. glauca		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	0.1
Herb-Dwarf Shrub Stratum: D		21	26	32	36	20	23	22	20	19	19	21	22	21	19	16	27	23
Myrica gale	-*	.	13	19	89	179	200	200	200	179	200	200	200	200	.	.	.	117
Carex aquatilis	+	100	200	89	89	100	200	27	100	.	89	100	27	2	2	100	19	78
Potentilla palustris	+	78	89	89	179	13	13	2	78	3	89	2	200	78	89	2	179	74
Ledum groenlandicum	*	.	.	.	.	179	179	100	89	63	89	200	2	63	.	.	.	60
Smilacina trifolia	+	3	.	2	2	78	19	2	179	.	179	3	23	.	2	.	78	36
Calla palustris	*	27	200	63	78	.	.	.	.	179	.	.	.	.	.	.	.	34
Carex retrorsa	+	2	.	78	89	.	.	2	.	100	.	.	.	78	100	.	19	29
Chamaedaphne calyculata	*	89	.	19	2	2	19	3	30	89	3	3	100	78	.	23	.	29
Carex diandra	*	89	.	89	100	2	19	2	4	63	19	4	23	2	3	19	.	27
Calamagrostis inexpansa		89	78	3	30	3	2	2	2	.	.	.	.	.	100	100	3	26
Lysimachia thyrsiflora	+	100	100	.	3	.	.	.	.	200	.	.	.	.	.	.	.	25
Calamagrostis canadensis		.	2	.	2	.	.	3	2	179	3	2	3	3	.	.	200	25
Larix laricina	*	.	.	.	.	155	78	63	.	.	23	3	2	.	.	.	.	20
Betula glandulosa		19	.	.	.	.	.	.	2	2	19	63	3	63	78	2	63	20
Utricularia vulgaris		100	78	89	2	.	.	.	.	.	.	.	.	.	.	.	.	17
Betula pumila	*	.	.	.	3	2	2	3	3	27	3	2	19	4	89	19	78	16
Carex limosa	*	.	.	78	2	2	78	.	.	.	.	3	19	19	2	23	19	15
Salix pedicellaris	*	.	89	19	.	19	13	.	3	19	23	4	2	19	27	.	.	15
Equisetum fluviatile		.	2	100	89	2	23	3	3	.	.	3	3	.	.	.	.	14
Oxycoccus microcarpus	+	.	.	.	.	30	2	27	30	2	2	100	5	27	.	3	.	14
Andromeda polifolia	*	.	.	19	.	89	89	2	19	.	.	.	.	3	.	.	3	14
Stellaria crassifolia	+	.	78	89	45	2	2	.	.	.	.	.	.	.	.	.	.	14
Carex disperma	*	.	.	78	23	.	2	.	.	3	19	3	2	78	2	2	3	13
Oxycoccus quadripetalus	*	.	.	2	.	.	100	2	2	.	89	2	2	2	.	.	.	13
Eriophorum angustifolium	*	.	78	100	23	.	.	.	.	.	.	.	.	.	.	.	.	13
Carex paupercula	*	3	.	78	23	3	.	.	27	3	4	3	3	23	3	.	19	12
Drosera rotundifolia	*	.	.	2	.	89	27	3	23	2	3	27	3	.	.	.	.	11
Salix pyrifolia		89	.	78	.	.	.	3	.	.	.	.	.	2	.	.	.	11
Epilobium palustre		19	2	13	30	.	2	.	.	.	.	2	3	89	3	3	3	11
Ranunculus gmelinii	+	3	23	89	30	2	2	2	3	.	.	.	3	.	.	2	2	10
Menyanthes trifoliata	*	.	30	100	30	.	.	.	.	.	.	.	.	.	.	.	.	10
Sium suave		.	100	19	4	.	.	.	.	27	.	.	.	.	.	.	.	9.4
Galium trifidum		23	30	19	30	.	.	.	.	3	.	.	.	.	3	.	30	8.6
Alnus tenuifolia		.	.	.	27	.	.	.	.	.	.	.	.	.	.	3	100	8.1
Fragaria vesca		.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	19	7.4
Typha latifolia		.	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6.2
Carex rostrata	+	.	89	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5.6
C. canescens	+	.	.	.	.	.	.	.	.	.	.	.	.	63	2	.	.	4.1
Salix barklayi (?)		.	.	.	63	.	.	.	.	.	.	.	.	.	.	.	.	3.9
Petasites vitifolius	+	.	.	.	.	.	.	.	.	.	.	.	.	.	63	.	.	3.9
Bidens cernua		23	27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3.1
Salix myrtillifolia	+	.	.	.	.	.	.	.	.	.	.	.	.	19	2	.	23	2.8
Cicuta douglasii	+	19	.	.	19	.	.	.	.	.	.	.	.	.	.	.	2	2.5
Sparganium minimum		.	13	.	19	.	.	.	.	.	.	.	.	.	.	.	.	2.0
Rubus chamaemorus	*	.	.	.	.	.	.	27	.	.	3	.	.	.	.	.	.	1.9
Pyrola asarifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23	1.4
Linnaea borealis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23	1.4
Mentha arvensis		.	.	.	19	.	.	.	.	.	.	.	.	.	.	.	4	1.4
Rumex occidentalis	*	2	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.3
Picea mariana	*	.	.	2	.	2	2	3	3	.	2	2	3	.	.	.	.	1.2
Arctostaphylos uva-ursi		.	.	.	.	.	.	.	.	19	.	.	.	.	.	.	.	1.2
Triglochin maritima		.	.	13	2	.	.	.	.	.	.	.	.	.	.	.	.	0.9
Stellaria longifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	4	0.6
Carex tenuiflora	*	.	.	4	.	.	2	.	.	.	.	.	.	.	.	.	.	0.4
Salix serissima	*	.	.	2	.	.	.	.	.	.	.	.	.	.	.	4	.	0.4
Myriophyllum exalbescens		.	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	0.4
Lemna minor		2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.3
Picea glauca		.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	3	0.3
Carex brunnescens	*	.	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Agropyron trachycaulum		.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2	0.2
Carex lasiocarpa	*	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Vaccinium vitis-idaea	*	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	0.2
Maianthemum canadense		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Pyrola secunda		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0.2
Sparganium eurycarpum	*	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.1
Carex tenera	*	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	0.1
Equisetum scirpoides		.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	0.1
E. sylvaticum		.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	0.1
Eriophorum brachyantherum	*	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	0.1

x̄ Mean.
A *Calla palustris* Subtype.
B *Larix laricina/L. laricina/Ledum groenlandicum* Subtype.
C *Alnus tenuifolia/Fragaria vesca* Subtype.
D Number of species.
[a] Prominence value (rounded off).
+ Species achieving their highest prominence values by stratum in this community type.
* Species by stratum exclusive to this community type.

ments occur within it along a complex (hollow-hummock) topographic-moisture gradient from subhygric to submesic. This ST is quite distinct with a low similarity (46%) to the third ST. It is comparable to the Regenerating and Mature Stages of the Sphagnum Bog Series of the *Larix laricina* Association of Moss (1953a,b).

The *Alnus tenuifolia/Fragaria vesca* ST is an overmature hummock phase composed of three communities (143, 144, 152; Table 29) representing a degenerating bog stage preceding the Wet Lowland Forest CT. This ST is characterized by hygric to submesic conditions having numerous upland species, and numerous relict and/or degenerating *Sphagnum* hummocks. It is comparable to the Degenerating Stages of the *Sphagnum* Bog Series of the *Picea mariana-Sphagnum* Association of Moss (1953a,b).

The mean number of vascular species per community is 25, the 4th highest recorded (Table 2). Two species in the tree stratum, nine in the shrub stratum, and 27 in the herb-dwarf shrub stratum are exclusive to this CT, and one species in the shrub stratum and 13 in the herb-dwarf shrub stratum have their highest mean PV's here (Table 29, App. 9). This type has a very poorly developed tree stratum, highly developed shrub stratum, and moderately developed herb-dwarf shrub stratum (Pl. 20). This CT has the highest moss cover and no liverworts (Table 2). Total understory biomass averages 3,400 kg/ha

Plate 20. *Larix laricina/Myrica gale/M. gale* community of the *M. gale/M. gale* (Bog) Community Type of zone 142 at site #2 in the Nuphar Lake study area.

(2nd highest recorded) with graminoids (37%) and mosses (30%) contributing most of the weight (Table 4). Representative age is 80 years, the 4th oldest CT (Table 19).

Tree Stratum

Average cover of this stratum is 9%. The mean number of species per community in this stratum is 0.8 (Table 2). *Larix laricina* is most prominent, followed closely by *Picea mariana* and *Salix arbusculoides*. The other two species, *P. glauca* and *Alnus tenuifolia*, are unimportant in this CT and occur in the immature and overmature hummock bog phases, respectively (Table 29). *Larix laricina* and *P. mariana* are exclusive to this CT (Table 29, App. 9). Total live basal area is 0.1 m^2/ha with *L. laricina* being the major contributor (no dead basal area reading; Table 16). No trees were recorded in the quadrats (Table 17). Total live and dead sapling densities are 290 and 180 stems/ha. *Salix arbusculoides* and *L. laricina* are the main contributors to live and dead densities respectively (Table 7). Average sapling height is 5.2 m for live and 3.4 m for dead individuals (Table 8). Average age of live trees is 78 years (Table 19), of saplings 41 years (Table 9).

Shrub Stratum

Average shrub cover is 68%, the same as in the Levee Tree CT. The mean number of species per community in this stratum is 8, the highest recorded (Table 2). *Myrica gale* is the most prominent of 18 species, followed by *Salix pedicellaris*, *Chamaedaphne calyculata*, and *Betula glandulosa*. Much less common are *B. pumila*, *Larix laricina*, *Ledum groenlandicum*, and *Picea mariana*. These species and *Andromeda polifolia* in this stratum are exclusive to this CT (Table 29, App. 9). Total live and dead shrub densities are 137,000 and 22,100 stems/ha with the former peaking here. *Myrica gale* is the main contributor to both densities (Table 10). The average height of live shrubs is 8 dm (Table 11); the average age of live shrubs is 12 years (Table 12).

Herb-Dwarf Shrub Stratum

This stratum is composed of 26 forbs, 21 graminoids, 19 woody species (highest recorded), and 3 horsetails. Ericaceous species attain their highest diversity and abundance in this CT (Table 29). The mean number of species per community in this stratum is 23, the same as in the Upland Forest CT. Average stratum cover is 60% (Table 2). *Myrica gale* is dominant, followed by *Carex aquatilis*, *Potentilla palustris*, and *Ledum groenlandicum* (Table 29). *Calla palustris*, *Chamaedaphne calyculata*, *Carex diandra*, and 24 other species in this stratum are

exclusive to this CT (Table 29, App. 9). Total live dwarf-shrub density is 41,800 stems/ha (2nd highest recorded) with *M. gale* the main contributor (Table 13).

b. Environment

This CT occurs in lowlands of the NL basin which is surrounded by Precambrian outcrops and high levees (Pl. 5). This CT has not been inundated by over-levee flooding in recent history, *i.e.* within the last 100 years. As the zones have an elevation of 0.2 m ASWL (range: 0-0.8 m), most if not all the zones are affected by the small water-level fluctuations occurring in Nuphar Lake during the growing season.

The very strongly (5.0) to medium acid (5.6) soils are exclusively organic with hydric and cryic components. The hydric component is present where the water table is at or immediately below the quaking moss mat in depressional to level areas. The soil moisture regime of this component is hydric to hygric. The cryic component occurred beneath sphagnum hummocks throughout the 1970 and 1971 growing seasons. The mean depth from hummock top to ice layer, which generally exceeds 15 cm in thickness, is 80 cm (range: 70-100 cm). Frozen soil attains its best expression under the larger sphagnum hummocks which averaged 20 cm in height (range: 10-50 cm). Microtopography ranges from nearly level to sharply hummocky. The soils have medium sodium, sulphate, and available nitrogen

values; low conductivity, calcium carbonate, and available phosphorus values; and very low available potassium values. Average profile organic content is high. Mean field soil moisture content is 950%, the highest recorded (range: 310-1810%), which is *ca*. 7x FC and 10x PWP. These relationships indicate an exceedingly high soil moisture surplus (continuous saturation) throughout the year. The extreme spatial variability in moisture content results from the discontinuous soil frost pockets, microrelief, and water-level relationships. Very poorly drained and cold soil conditions prevail in this CT.

c. Integration

This CT occupies the hygric to mesic range of the moisture gradient. Species exclusive to this CT and those with the highest prominence here (Table 29, App. 9) are categorized as "hygrophytic". These species achieve the highest prominence in this CT because of the inability of flood waters to over-top the highly developed levees surrounding the NL basin. This lack of flooding has resulted in a CT characterized by high accumulations of sphagnum mosses, organic matter, and soil moisture, and by low pH values and nutrient contents (App. 2,3). These conditions have produced ombrotrophic and oligotrophic states which appear well within the tolerance of the above species. With the exception of nitrogen, the major nutrients of this CT have relatively low values compared to

other CT's, perhaps reflecting the slow rates of chemical reactions caused by low soil temperatures. The medium nitrogen values of this CT appear to be the result of the high availability of nitrogen-fixing symbiotic bacteria associated with *Myrica gale* in certain zones (Odum 1971). The production of nitrogen may be important to the presence and abundance of meadow species as well as certain bog species in the immature hummock phase. Although most species in the study region appear to tolerate a wide range of soil acidity, the strongly acidic soils of this CT probably exclude most wetland species. However, high organic and soil moisture contents ensure the elimination of all but a very few upland species which may invade the tops of mature and degenerate hummocks. The maturation of sphagnum hummocks has resulted in a microtopographic mosaic producing micro-environments which exhibit the wide range of moisture conditions allowing the existence of numerous species alignments according to moisture tolerances.

These species appear well-adapted to the lowest soil temperatures recorded in the study region. In conjunction with a sheltered location, the development of a thick insulating layer of organic matter assures, by reducing the effects of incident solar radiation, the maintenance of frozen soil, and consequently low temperatures, *e.g.* within 22 cm of a hummock top, a 6 C^{o} drop in

temperature was recorded. Presence of frozen soil in sphagnum dominated areas probably eliminates all meadow and some bog species which are cold intolerant.

The presence of a very poorly developed tree stratum has exclusively restricted more shade tolerant bog species to the Wet Lowland Forest CT. This very poor development may reflect the near-surface presence of soil frost which restricts root distributions.

The presence of peripheral rather than heart rot in *Betula papyrifera* specimens at the junction of the Bog and Upland Forest CT's suggests that a rise in basin water levels occurred long ago and has been maintained, at slightly lower levels, for some time. This rise in water levels was most likely accomplished through active construction of dams by beavers. These dams and the absence of over-levee flooding have probably encouraged the development and maintenance of the Bog CT.

Vegetational and environmental characteristics suggest that the immature and overmature hummock phases are intermediate stages and the mature hummock phase a late terminal stage, all controlled by autogenic factors. This highly distinct CT is comparable to the Bog Shrub Association of Raup (1935), the *Picea mariana* and *Larix laricina* Associations of Moss (1953a), and the Open, Severely Restricted Drainage CT of the Standing Water Landscape Type of Dirschl *et al.* (1974).

17. Precambrian Outcrop CT's

These CT's are included in the thesis to illustrate the wide range of floristic and vegetational variation in the study region. Because attention was not focused on xerarch succession, no quantitative vegetation analysis was conducted in this CT.

a. Vegetation

The outcrop flora is very distinctive, having more exclusive species than any of the previously described CT's. Many outcrop species are associated with the Prairie and Cordilleran Regions, while a few such as *Dryopteris fragans* and *Silene antirrhina* are exclusive in Alberta to the PA delta and surrounding area. The latter species has not yet been recorded elsewhere in Alberta (Table 30). The outcrop vegetation may be split into three different CT's, here tentatively recognized in the absence of quantitative data (Pl. 21). These CT's are very common only on outcrops of all study areas.

1. *Pinus banksiana/Juniperus communis/ Arctostaphylos uva-ursi* CT (tentative)

This is the most poorly developed CT. It has an open, sparse physiognomy displaying mostly a contagious dispersion pattern. This CT, occurring on exposed crests and slopes of outcrops, is similar to those on outwash sands and shield rocks north and south of the study region but not much further east. Mosses and lichens are

Table 30. Flora of three tentatively recognized community types on Precambrian Outcrops of the study region. Species presence is indicated by a '+'.

Species Composition		Community Type 1	2	3
Tree Stratum				
Pinus banksiana	*	+	.	.
Prunus pensylvanica	*	.	+	.
Picea glauca		.	+	+
Populus tremuloides		.	+	+
Betula papyrifera		.	+	+
Salix bebbiana		.	.	+
Shrub Stratum				
Juniperus communis	*	+	.	.
J. horizontalis	*	+	.	.
Pinus banksiana	*	+	.	.
Arctostaphylos uva-ursi		+	.	.
Populus tremuloides		+	+	+
Betula papyrifera		+	+	+
Shepherdia canadensis		+	+	+
Symphoricarpos albus		+	+	+
Viburnum edule		+	+	+
Prunus pensylvanica	*	.	+	.
Picea glauca		.	+	+
Salix bebbiana		.	+	+
Alnus crispa	*	.	+	+
Ribes oxyacanthoides		.	+	+
Amelanchier alnifolia		.	+	+
Rosa acicularis		.	+	+
Rubus strigosus		.	+	+
Vaccinium vitis-idaea		.	+	+
Ribes lacustre		.	.	+
Herb-Dwarf Shrub Stratum				
Agropyron trachycaulum		+	.	.
Agrostis scabra		+	.	.
Saxifraga tricuspidata	a	+	.	.
Poa interior	b	+	.	.
Achillea millefolium	b	+	.	.
Cryptogramma crispa	*	+	.	.
Lycopodium complanatum	*	+	.	.
Festuca saximontana	*	+	.	.
Oryzopsis pungens	*	+	.	.
Trisetum spicatum	*	+	.	.
Carex foenea	*	+	.	.
Corydalis aurea	*	+	.	.
C. sempervirens	*	+	.	.
Arabis divaricarpa	*	+	.	.
A. hirsuta	*	+	.	.
A. holboellii	*	+	.	.
Potentilla tridentata	*	+	.	.
Apocynum androsaemifolium	*	+	.	.

Potentilla arguta	[illegible]	+		
Androsace septentrionalis	*	+	·	·
Polygonum douglasii	*	+	·	·
Cerastium vulgatum	*	+	·	·
Aster falcatus	*	+	·	·
Campanula rotundifolia		+	+	·
Hierochloe odorata	*	+	+	·
Stellaria longipes	*	+	+	·
Elymus innovatus		+	+	+
Fragaria virginiana		+	+	+
Potentilla norvegica		+	+	+
Geranium bicknellii		+	+	+
Solidago lepida		+	+	+
Potentilla pensylvanica		+	+	+
Solidago decumbens	*	+	+	+
Cystopteris fragilis	*	·	+	·
Goodyera repens	*	·	+	·
Polypodium vulgare		·	+	+
Maianthemum canadense		·	+	+
Sisyrinchium montanum		·	+	+
Geocaulon lividum		·	+	+
Parnassia palustris		·	+	+
Rubus pubescens		·	+	+
Lathyrus ochroleucus		·	+	+
Vicia americana		·	+	+
Aralia nudicaulis		·	+	+
Pyrola virens		·	+	+
Galium boreale		·	+	+
Linnaea borealis		·	+	+
Astragalus eucosmus	*	·	+	+
Vaccinium myrtilloides	*		·	+
Veronica peregrina	*	·	·	+
Arnica lonchophylla		·	·	+
Poa palustris		·	·	+
Actaea rubra		·		+
Anemone canadensis		·	·	+
Mitella nuda		·	·	+
[illegible]				+
Geum allepicum			·	+
Rubus acaulis		·		+
Cornus canadensis			·	+
Pyrola asarifolia		·	·	+
P. secunda		·		+
Mertensia paniculata				+
Galium triflorum		·		+
Calypso bulbosa	*		·	+
Woodsia ilvensis	*			+

Pinus banksiana/Juniperus communis/Arctostaphylos uva-ursi Community Type (tentative).
[illegible]
Type (tentative).

[illegible] exclusive to the [illegible]

Plate 21. An example of a Precambrian Outcrop Community Type adjacent to the Rivière des Rochers near the entrance to the Lake Athabasca Marsh study area.

abundant in this CT.

Tree cover is very low, provided solely by *Pinus banksiana* (Table 30). The average tree height is 8 m, with the representative age being 54 years.

Shrub cover is low, provided by *Pinus banksiana*, *Juniperus communis*, *J. horizontalis*, and other species (Table 30). Average shrub height is 1 m, with the age being 35 years.

The herb-dwarf shrub stratum has many species (Table 30), but most have low covers.

This CT is comparable to the Pine-Heath Faciation of the *Pinus banksiana* Consociation of Moss (1955) and the Grassland CT of the Precambrian Outcrop Landscape Type of Dirschl *et al*. (1974).

2. *Picea glauca/Rosa acicularis/Vaccinium myrtilloides* CT (tentative)

This CT is structurally better than the preceding type by having higher densities and covers in the shrub and tree strata. It is located on sheltered crests and slopes of outcrops. *Pinus banksiana* forests north and east of the study region have this type. Moss and lichen cover is less abundant here.

Tree cover is moderate, provided by *Picea glauca*, *Populus tremuloides*, and *Prunus pensylvanica*. The average tree height is 8 m, with the representative age being 51 years.

Shrub cover is moderate, provided by *Rosa acicularis*, *Prunus pensylvanica*, and other species. Average shrub height is 1 m, with the age being 22 years.

Herb-dwarf shrub cover is low, provided by a relatively small number of species such as *Goodyera repens* and *Cystopteris fragilis*.

This CT is comparable to the Forest CT of the Precambrian Outcrop Landscape Type of Dirschl *et al.* (1974).

3. *Picea glauca/Alnus crispa/Cornus canadensis* CT (tentative)

This is structurally the best developed CT, having higher species abundance and cover in all strata. It is located along sheltered bases and in pockets of granitic outcrops, where soil moisture is more plentiful. *Pinus banksiana* forests north and east of the study region also have this type. Unlike lichens, mosses are as abundant here as in the first CT.

Tree cover is high, provided by *Picea glauca*, *Populus tremuloides*, and *Salix bebbiana*. The average tree height is 14 m, with the representative age being 110 years.

Shrub cover is high, provided by tall species such as *Alnus crispa* and low species such as *Ribes lacustre* and *Viburnum edule* (Table 30). The average shrub height is 2 m, with the age being 28 years.

Herb-dwarf shrub cover is very high, provided by such species as *Actaea rubra*, *Woodsia ilvensis*, and

Calypso bulbosa.

This CT is comparable to the Forest CT of the Precambrian Outcrop Landscape Type of Dirschl *et al.* (1974).

b. Environment

These CT's occur in varying extent in all study areas. They are never flooded, being located well above the historical maximum flood levels. The complex topography is extremely variable ranging from nearly level to very hilly sites which have a relief varying up to 50 m.

The very strongly (4.9) to strongly acid (5.5) mid-slope soils appear to be dominated by Lithic Humo-Ferric Podzols. These soils have the highest available phosphorus in the study region, with nitrogen considered medium, and potassium low. The influence of granitic parent materials is shown by the low pH and calcium carbonate values. These soils are considered to have a moderate nutrient status attained mainly through the collection from upslope areas of run-off having high concentrations of leachates from leaf-drip and numerous bison and wolf droppings. The low sodium, conductivity, sulphate, and available potassium values probably reflect the lack of flooding.

Soils in depressions and on moderate slopes are better-developed and more nutrient rich than soils on upper slopes and ridges. The latter soils are poorly developed because of selective environmental controls

which, directly or indirectly, limit the *in situ* accumulation of organic matter and nutrients.

Profile organic matter is generally low, and slightly less than that of the Upland Forest CT. The sampled soil profiles have mainly sandy loams with sand the dominant fraction. The S/C ratio is 29, the highest recorded in the study region. The low organic matter, moderate sand content, and variable slopes frequently exceeding 60% combine to give a soil moisture content of 10%, the lowest recorded in the study region. This value is *ca.* half FC and 1x PWP. These relationships indicate a low (low refers to field soil moisture contents *ca.* half FC and <2x PWP) moisture content derived solely from local precipitation. This conclusion is substantiated by soil samples taken during the 1971 growing season. The high variability in soil moisture reflects the profound effect slope angle and aspect have on drainage and evapotranspiration, and consequently the ability of moisture demanding plants to live on these soils. Moderately well- to rapidly-drained conditions prevail on the outcrops.

c. Integration

Depending on the degree of exposure and topographic position, the three tentatively recognized CT's occupy three broad segments of the outcrop moisture gradient from xeric to mesic conditions which are, in turn, reflected by changes in their species compositions, as shown in Table 30.

Species of the first CT must tolerate long periods of low soil moisture and drought, high incident radiation, dessication from sustained and frequently high wind velocities, wide fluctuations in air and soil temperatures and, in many cases, poor soil development and nutrient status.

Species of the third CT must tolerate short periods of high run-off, high soil moisture, and deep shade. Most of the factors controlling species occurrences in the xerophytic type are not operative in this mesic type. Thus, the climate has been ameliorated by topographic location and community structure.

The second CT is characterized by subxeric to submesic conditions. It therefore falls between the former xeric and mesic types, sharing many of the environmental features of both groups. Species appear well-adapted to the environment of this intermediate CT.

Several species have broad tolerances to the environmental conditions occurring on rock outcrops in the study region. *Campanula rotundifolia* and *Hierochloa odorata* occur in the first and second CT's and seem intolerant of complete shade and high soil moisture. On the other hand, species occurring in the second and third CT's such as *Picea glauca* in the tree stratum, *Ribes oxyacanthoides* in the shrub stratum, and *Lathyrus ochroleucus* in the herb-dwarf shrub stratum can tolerate wide

variations in soil moisture and light requirements but appear sensitive to extreme drought and incident radiation. Species groups represented by *Populus tremuloides* in the shrub stratum and *Elymus innovatus* in the herb-dwarf shrub stratum occur in all three CT's. These species seem to tolerate wide variations in environmental conditions. The physical environment of the three Precambrian Outcrop CT's appears to be the most unfavourable encountered in the study region, with the probable exception of the Levee Herb CT.

The three Precambrian Outcrop CT's are comparable to the Granitic Hills Flora of Raup (1935) and the Rock Outcrop Habitat Type of Townsend (1973b). The *Pinus banksiana/Juniperus communis/Arctostaphylos uva-ursi* CT (tentative) appears to represent an edaphic climax on Precambrian outcrops. The other two CT's seem to represent seral stages toward the Upland Forest CT.

F. Flora of Disturbed Areas

Species associated with naturally and man-disturbed areas of the study region are given in Table 31. Five of these species have not been previously recorded for the PA delta. These mostly light-demanding species show different tolerances to unstable conditions. They usually display excellent asexual and/or sexual reproduction which ensures their success in a constantly changing

Table 31. Partial list of the flora associated with naturally and man-disturbed areas in the study region. Species presence is indicated by a '+'.

Species		Natural Disturbances			Disturbances by Man	
		Shorelines[a]	Alluvial Terraces	Forest Clearings and Paths	Clearings[b]	Plots[c]
Equisetum arvense		.	+	.	.	+
E. palustre		.	.	.	.	+
Agrostis scabra		.	+	.	+	+
Beckmannia syzigachne		.	.	.	.	+
Bromus pumpellianus		.	.	+	.	.
Calamagrostis canadensis		.	+	+	.	.
C. purpurascens		.	.	+	.	.
Danthonia intermedia		.	.	+	.	.
Elymus innovatus		.	.	+	.	.
Hordeum jubatum		.	+	.	.	.
Poa pratensis		.	.	+	.	.
Trisetum spicatum		.	.	+	.	.
Carex atherodes		.	.	.	.	+
Urtica gracilis		.	.	+	.	.
Polygonum aviculare		.	+	.	.	+
P. convolvulus		.	.	.	+	.
P. lapathifolium		+	.	.	.	.
Rumex maritimus		.	+	.	.	.
Chenopodium album		+	.	.	.	.
C. capitatum		.	+	.	.	.
C. leptophyllum		+	+	.	.	.
Kochia scoparia		+	.	.	.	.
Stellaria longifolia		.	.	.	.	+
Ranunculus flammula	*	+	.	.	.	.
R. macounii		.	.	.	.	+
R. sceleratus		.	+	.	.	.
Capsella bursa-pastoris		.	.	.	+	.
Descurainia richardsonii		.	.	.	+	.
Erysimum cheiranthoides		.	+	.	.	.
Rorippa islandica		.	+	.	+	.
Thlaspi arvense		.	.	.	+	.
Fragaria vesca		.	.	.	.	+
Geum allepicum		.	.	+	.	.
G. macrophyllum		.	.	+	.	.
Potentilla anserina		.	+	.	.	.
P. norvegica		.	.	.	+	+
Astragalus alpinus		+	.	.	.	.
Medicago sativa	*	.	.	.	+	.
Melilotus alba	*	+	+	.	+	.
Trifolium repens		.	+	.	+	.
Geranium bicknellii		.	.	+	+	.
Epilobium angustifolium		.	+	+	+	.
Oenothera biennis	*	+	.	.	.	.
Gentianella amarella		.	.	+	.	.
Collomia linearis		.	.	+	.	.
Mertensia paniculata		.	.	+	.	.
Dracocephalum nuttallii		.	.	.	.	+
Mentha arvensis		.	.	.	+	+
Plantago major		.	+	.	.	.
Galium trifidum		.	.	.	+	+
Lonicera dioica		.	.	+	.	.
Achillea millefolium		.	.	.	+	.
A. sibirica		.	.	+	.	.
Antennaria rosea		.	.	+	.	.
Artemisia biennis		.	+	.	.	.
Aster ciliolatus		.	.	+	.	.
A. falcatus		.	.	+	.	.
Erigeron philadelphicus		.	.	+	.	.
Hieracium umbellatum	*	.	.	+	.	.
Taraxacum officinale		.	+	.	+	+

a Gravel, sand, and mud.
b Paths, fields, and cabins.
c Cleared for biomass sampling.
* New species record for the PA delta based on species lists of Raup (1935) and Gentle (1973).

environment. In general, flooding and its associated effects are the controlling disturbance factors in shorelines and alluvial terraces of the study region, while bison trampling and windfall are important influences in forests. Pyric disturbances do not appear as important in the study region as they are in sections of the old delta. Species around cabins, pastures and fields, and hunting paths appear to be the result of man's activities. The majority must have been introduced by man from similar locations around Fort Chipewyan and other settlements. Plots cleared for biomass sampling were later visited to note species presence and cover. Generally the species with the best vitality in a particular zone invaded the cleared plot of that zone. Species associated with perturbed areas are relatively transitory, giving way to species more characteristic of stable environments when disturbing factors have decreased or ceased.

G. Synthesis

The 16 CT's represent the typical variation found in the vegetation of low deltaic areas in the study region. All are dependent upon landscape features such that each CT attains its best expression in a different physiographic position. Physiographic features and geomorphological processes are thus the primary controls for CT's in the total vegetation of the study region. The 16

CT's are also dynamically controlled and interrelated as will be shown in the next section. The CT's fluctuate around distinct positions in dynamic equilibrium with allogenic environmental and autogenic biological controls. The relative importance of these controls is reflected in the extent, stability, and distribution patterns of the CT's.

The three tentatively recognized Precambrian Outcrop CT's have rigidly controlled environments which contrast sharply with the harsh hydric-to-xeric environment of the Levee Herb CT. Thus the environments of these two types represent the stable and unstable extremes encountered in the study region.

II COMMUNITY DYNAMICS

According to Daubenmire (1968:201), successional sequences can be initiated by either allogenic or autogenic factors, as all seres, regardless of the relative importance and degree of interaction of these two factor groups, involve changes in the environment and vegetation. The result of his "environmental metamorphosis" in both cases is a terminal community of relative stability. Odum (1969) has characterized the successional changes that occur in community structure and function from developmental stages to mature stages. Daubenmire discounts the

practice of some ecologists to consider as "true" succession only autogenically initiated and directed seres because this conceptually narrower view would unnecessarily complicate and restrict the study of vegetation dynamics. The author, in supporting Daubenmire's approach, believes that physiography is important in determining which factors will initiate a successional sequence. The general tendency is for allogenic, polygenic, and autogenic factors to initiate succession in active, semi-active, and inactive areas of the study region, respectively. This chapter attempts to identify the successional factors controlling concrete communities, and consequently their abstract CT's, by examination of soils, hydrologic regime, and species' autecologies.

Successional trends in the study region may be divided, on the basis of important differences in environmental and vegetational characteristics and in geomorphological processes, into five major sequences corresponding to the five different study areas. The sequences of CT's represent states of equilibrium under existing conditions among the sites. The sequences are both environmental and dynamic "coenoclines" subject to allogenic and autogenic controls (Whittaker 1975). A successional diagram for each study area has been proposed in which major species are positioned according to their CT's and time. Each community replacement is based on the following

criteria: 1) community position in the site; 2) Sørensen's co-efficient of similarity values; 3) densities of dwarf-shrubs, shrubs, saplings, and trees; 4) ages of shrubs, saplings, and trees; and 5) vigor and vitality of prominent species. These criteria were used to confirm whether communities being compared were dynamically related, as juxtaposition within a site is not an infallible indication of possible successional relationships.

Replacement patterns vary somewhat among sites in a study area, *i.e.* communities may be absent from one or more sites but present in others. The result is a successional mosaic of community trends. The approximate number of growing seasons for each community replacement has been calculated and is believed to be of the right order. This estimate of successional rate is based on ages obtained from disc and core samples of shrub and tree individuals. Each estimate reflects the number of years required for a succeeding community to achieve its fullest expression. If there is an intermediate community in the sequence, the time required for replacement to occur may vary considerably from the more direct route. Temporal variations reflect differences in ages of prominent species and of total species composition in communities.

The successional diagrams in the following sections for study areas give the "normal" species replacement

sequences in exposed and sheltered areas during relatively stable or seasonally declining water-levels. Only major species which attained sufficient prominence to be named as part of one or more communities in each CT were considered by the author for illustrating species replacement patterns in each study area. When a dwarf-shrub species was named as part of a community, the author selected the next most prominent herb species to illustrate replacement patterns. There were only limited data available for community changes in CT's which experienced flooding during the study. Thus, retrogressive trends which may occur during periods of prolonged flooding are not illustrated or assessed in the diagrams. Intensive study of such trends remains to be done over much of the PA delta.

From a general successional viewpoint, CT's previously designated as being influenced primarily by allogenic, polygenic, and autogenic factors generally correspond to pioneer (PS), transitional(TrS), and terminal (TeS) stages, respectively. A further division of these stages into early (E), intermediate (I), and late (L) substages is made to clarify successional relationships of species and communities.

In the concluding section a successional diagram for the study region as a whole is presented in which the replacement relations among CT's are indicated, as well as their relations to soil moisture, flood frequency, and successional factors.

A. Successional Sequences in the Revillon Coupé Study Area

i. Introduction

Seven CT's, having 54 zones, are represented among the four sites sampled in this study area (see Fig. 3, p. 93; Pl. 1, p. 6). Islands and levees are the main landforms in this area.

ii. Succession

The prevailing successional sequences along flowing channels is shown in Figure 4. Three distinct sequences are evident in the RC successional diagram. In the lowest and most sheltered sections of this study area, *Typha latifolia* is the initial colonizing herb species, followed by *Eleocharis palustris* and later by *Equisetum fluviatile*. These three species dominate the EPS. *Epilobium angustifolium* dominates in the IPS; followed by *Mentha arvensis* and then *Equisetum pratense* in the LPS.

In the less sheltered study sites, *Eleocharis palustris*, *Juncus alpinus*, and *Carex aquatilis* are the initial colonizing herbs of the EPS. They are replaced first by *Rorippa islandica* and later *Equisetum palustre* in the EPS. The latter species is followed by *E. pratense* in the IPS and LPS.

In the lowest and most exposed sections, *Equisetum arvense* is the initial colonizing herb of the EPS, replaced by *E. palustre* and later by *E. pratense* in the LPS. The latter is replaced by *Fragaria vesca* in the TrS, followed

Figure 4. Successional diagram for the Revillon Coupé study area, showing the sequence of community and soil types and the major species' replacements in the three vascular strata[a]. Refer to p. 238 for method of determining species replacements.

Legend:

Aln ten: *Alnus tenuifolia*
Car aqu: *Carex aquatilis*
Cor can: *Cornus canadensis*
Cor sto: *Cornus stolonifera*
Ele pal: *Eleocharis palustris*
Epi ang: *Epilobium angustifolium*
Equ arv: *Equisetum arvense*
Equ flu: *Equisetum fluviatile*
Equ pal: *Equisetum palustre*
Equ pra: *Equisetum pratense*
Fra ves: *Fragaria vesca*
Jun alp: *Juncus alpinus*
Men arv: *Mentha arvensis*
Pic gla: *Picea glauca*
Pop bal: *Populus balsamifera*
Ror isl: *Rorippa islandica*
Ros aci: *Rosa acicularis*
Pyr asa: *Pyrola asarifolia*
Sal beb: *Salix bebbiana*
Sal int: *Salix interior*
Sal lut: *Salix lutea*
Sal pse: *Salix pseudomonticola*
Sal pyr: *Salix pyrifolia*
Typ lat: *Typha latifolia*

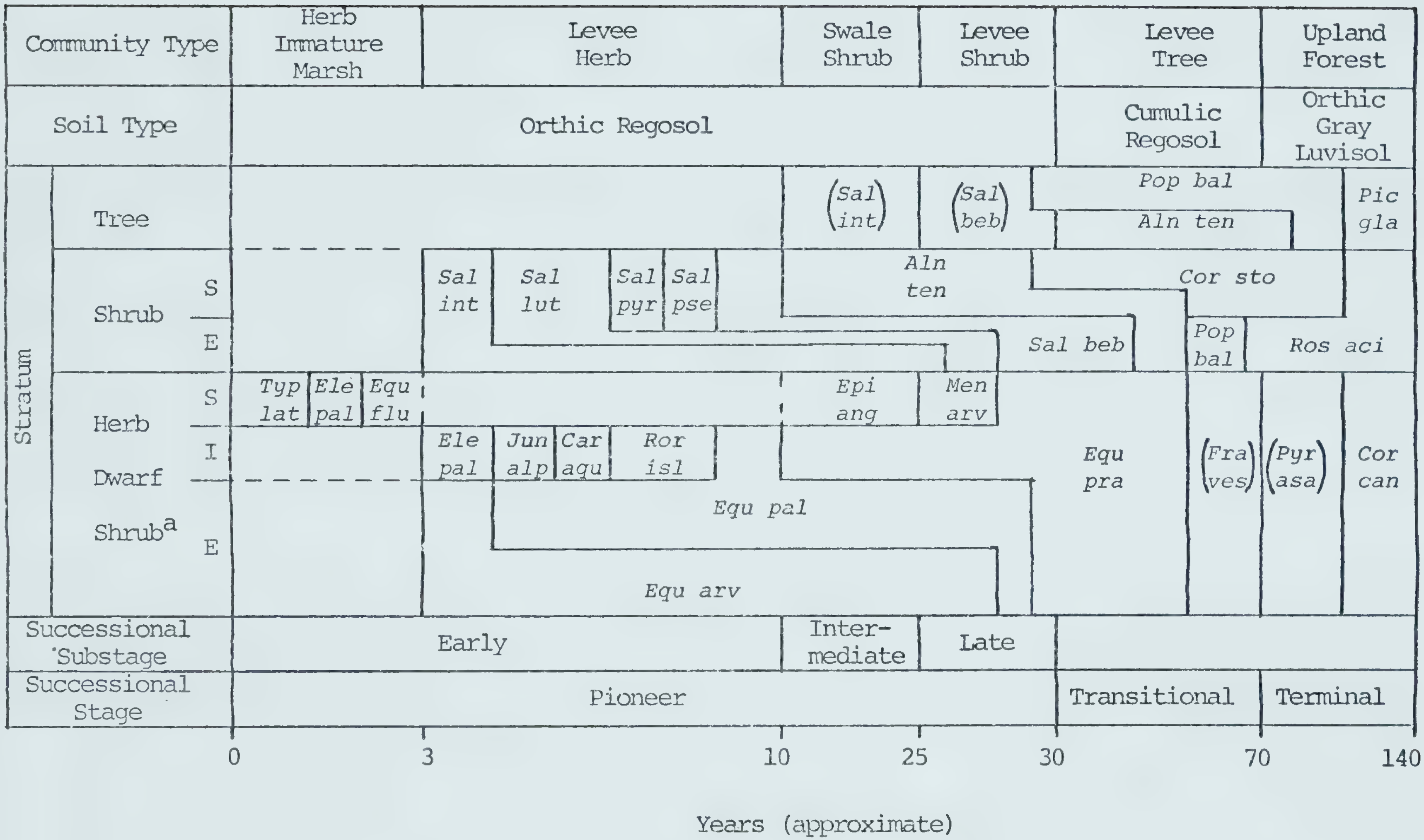
[a] Dwarf shrubs have been omitted from the herb-dwarf shrub stratum.

S: Sheltered areas.

I: Intermediate areas.

E: Exposed areas.

(): Species sometimes absent.



Community Type
Herb Immature Marsh
Levee Herb
Swale Shrub
Levee Shrub
Levee Tree
Upland Forest
Soil Type
Orthic Regosol
Cumulic Regosol
Orthic Gray Luvisol
Stratum
Tree
Shrub
Herb
Dwarf Shrub[a]
S
E
S
I
E
Sal int
Sal beb
Pop bal
Aln ten
Pic gla
Sal int
Sal lut
Sal pyr
Sal pse
Aln ten
Cor sto
Sal beb
Pop bal
Ros aci
Typ lat
Ele pal
Equ flu
Epi ang
Men arv
Ele pal
Jun alp
Car aqu
Ror isl
Equ pal
Equ arv
Equ pra
Fra ves
Pyr asa
Cor can
Successional Substage
Early
Inter-mediate
Late
Successional Stage
Pioneer
Transitional
Terminal
0
3
10
25
30
70
140
Years (approximate)

by *Pyrola asarifolia* and then *Cornus canadensis* in the TeS.

Salix interior is the initial colonizing shrub, followed by *S. lutea*. The latter is replaced in more sheltered areas of the EPS by *Salix pyrifolia*, *S. pseudomonticola*, and then *S. bebbiana*. *Salix lutea* is eventually replaced in more exposed levee areas by *S. bebbiana* in the LPS. *Salix bebbiana* is followed, usually in the TrS, by *Alnus tenuifolia* and later by *Cornus stolonifera* or *Populus balsamifera*. The latter species are replaced by *Rosa acicularis* in the TeS.

Salix interior is the initial tree species, found in the IPS: it is followed by *S. bebbiana* in the LPS and later usually by *Alnus tenuifolia* in the TrS and then *Populus balsamifera* in the TeS. The latter species is succeeded by *Picea glauca*, the terminal species of this study area.

For the herb-dwarf shrub stratum, Raup (1935:88) recognized only *Equisetum palustre*, *E. fluviatile*, and *E. pratense* in his successional sequence for local river deposits, which also includes *E. hyemale*. The latter species occurs in this study area but does not attain sufficient prominence to be named as part of a community by the author. Dirschl *et al*. (1974:30) recognized only *E. fluviatile*, *E. pratense*, and *Eleocharis* spp. However, *Glyceria* spp. which were not observed in the study area were included in Dirschl's sequence.

For the shrub stratum, Raup recognized only *Salix*

interior and *S. lutea*. Dirschl recognized *S. interior, S. bebbiana*, and *S. discolor*. The latter species was not recorded in this or any other study area.

For the tree stratum, Raup recognized the following sequence having two complexes: *Populus-Salix-Alnus* ⟶ *Populus-Picea* ⟶ *Picea*. In this investigation only one complex (*Populus balsamifera-Alnus tenuifolia*) has attained sufficient prominence to be named as part of a community by the author; other complexes are probably present but of lesser prominence. Dirschl recognized the following two complexes: *P. balsamifera-Salix bebbiana* ⟶ *Picea glauca-Abies balsamea*. The latter species does not occur in the study region. Both Raup and Dirschl did not mention *S. interior* in its sapling form (See Methods p. 19). Differences among sequences of this and previous investigations may be the result of the intensive and quantitative nature of this study and also its location in the northeastern portion of the PA delta.

Population analysis of major tree species (Table 32) along the successional sequence indicate that environmental conditions in Algal Aquatic and low-lying Herb Immature Marsh CT's exclude all species. However, conditions for trees improve in Swale Shrub and Levee Herb CT's. In the former, both *Picea glauca* and *Populus balsamifera* have *ca.* 14x more seedlings than in the latter. *Salix bebbiana* does well in the Levee Herb CT while *Alnus tenuifolia* seems to do much better in the Swale Shrub CT. Woody

Table 32. Mean densities per hectare of stem size classes of major tree species in five community types along the upper segment of the successional gradient in the Revillon Coupé study area.

Tree	SC[a]	Community Type[b,c]				
		10	9	11	12	13
		3	*19*	*12*	*8*	*3*
Picea glauca	sdl[d]	9330	630	2500	750	2670
	trs	.	.	.	.	500
	sap	.	.	.	30	27
	1	.	.	.	30	27
	2	.	.	.	.	27
	3	.	.	.	.	.
	4	.	.	.	.	80
	5	.	.	.	.	.
	6	.	.	.	.	27
	7	.	.	.	.	.
	8	.	.	.	.	.
	9	.	.	.	.	27
Populus balsamifera	sdl	1330	100	1830	1250	.
	trs	.	.	2120	3620	1330
	sap	.	.	33	120	107
	1	.	.	27	40	27
	2	.	.	27	90	80
	3	.	.	7	110	107
	4	.	.	.	130	27
	5	.	.	.	140	53
	6	.	.	.	80	27
	7	.	.	.	50	.
	8	.	.	.	10	.
	9	.	.	.	10	.
	10	.	.	.	.	.
	11	.	.	.	10	.
Salix bebbiana	sdl	4670	4420	2830	250	667
	trs	.	320	5460	560	330
	sap	.	.	220	20	53
	1	.	.	140	10	.
Alnus tenuifolia	sdl	8670	100	3500	1500	1330
	trs	61300	.	38300	3500	1330
	sap	.	.	200	1130	373
	1	.	.	20	510	27
	2	.	.	.	10	.

[a] Size Class.
[b] Community Type: 10) Swale Shrub, 9) Levee Herb, 11) Levee Shrub, 12) Levee Tree, 13) Upland Forest.
[c] Number of zones in the study area given in italicized numbers.
[d] sdl = seedlings; trs = transgressives; sap = saplings; and tree dbh classes: 1 = 8-13, 2 = 13-18, 3 = 18-23, 4 = 23-28, 5 = 28-33, 6 = 33-38, 7 = 38-43, 8 = 43-48, 9 = 48-53, 10 = 53-58, 11 = 58-63 cm.

stems of all species exhibit pronounced mortality, and short life-spans in these CT's. Environmental conditions in the Levee Shrub CT appear more conducive for tree development of *A. tenuifolia*, *S. bebbiana*, and *P. balsamifera*. The latter develops into a medium-sized tree while the first two just extend to small-sized trees. *Salix bebbiana* attains its best growth in this CT. In the Levee Tree CT, the tree stratum is very highly developed. *Alnus* and *Populus* exhibit their best growth in this CT. The latter demonstrates its excellent asexual reproductive capacity with a peak in the transgressive class and a hollow in dbh class 1, which correspond to the hollow and peak in the *P. glauca* population curve. In the Upland Forest CT, *P. glauca* reveals its best growth. This species exhibits an episodic regeneration pattern, as evidenced by the lack of stems in dbh classes 3, 5, 7, and 8. *Picea glauca* is the only tree species showing sustained regeneration and thus an ability to be self-perpetuating and in equilibrium with environmental factors of the Upland Forest CT. *Picea* seedlings colonize open areas with moderate herb cover on sandy loan and loam mineral soils with an overlying mor layer. Although seedlings are located above most annual floods, they appear to be tolerant of sediment-free flood-waters of short durations if moderately well-drained conditions are normally present. The mineral soil seedbed provided by flood and deposition of sediment may favour colonization of spruce in all the previous CT's. Transgressives and saplings of *Picea* seem more sensitive to flooding and strong light as they only occur in rarely flooded zones

having a moderate to highly developed overstory of *P. balsamifera*, *A. tenuifolia*, and *S. bebbiana*. Deadfalls from the *Populus* canopy create suitable seedbed conditions for *P. glauca* growth, *i.e.* on decaying tree stumps and stems, and eventual emergence into the open canopy. *Populus* lacks sustained regenerative capacity in the Upland Forest CT compared to *Picea*. These observations support those of Jeffrey (1964), Lacate (1965), and Gill (1971).

Tree Stratum (Table 33)

This stratum is found in allogenic Swale Shrub and Levee Shrub; polygenic Levee Tree; and autogenic Upland Forest CT's. The Levee Tree CT has the highest tree stratum cover, from predominantly deciduous species. Total tree cover appears to be positively associated with height above MSWL; available soil potassium; and total lichen and shrub covers, and negatively with flood-water duration; soil moisture; available water; and total bare ground cover.

Average tree species richness per zone increases throughout the successional sequence, peaking in the Upland Forest CT, and seems positively associated with height above MSWL; total lichen and tree covers; bryoid biomass; and representative age, and negatively with flood-water duration and available water. These relationships suggest that increases in tree species diversity may reflect decreased flooding and its related

[illegible] characteristics of community types along the successional gradient in the Revillon Coupé study area.

[illegible]	Community Type[illegible]						
	1	3	9	10	11	12	13
	5	4	3	14	12	8	3
[illegible]							
[illegible]	---[1]	[illegible].5	[illegible]	[illegible]	[illegible]	5.6	[illegible]
[illegible]	---	[illegible].2	[illegible]	[illegible]	[illegible]	5.8	[illegible]
[illegible]	---	58	[illegible]	71	[illegible]7	[illegible]	[illegible]
[illegible]	---	33	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	--	9	1		[illegible]	[illegible]	[illegible]
[illegible] %	---	34	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] %	---	32	31	[illegible]	[illegible]	16	[illegible]
[illegible]	--	[illegible]	7		[illegible]	[illegible]	[illegible]
[illegible]	---	[illegible]	4	1[illegible]	[illegible]	[illegible]	1.
[illegible]	---	3.[illegible]	4.0	[illegible]	[illegible]	3.[illegible]	[illegible]
[illegible]							
[illegible]	---	5.[illegible]	5.6	[illegible]	.3	2.[illegible]	1.[illegible]
[illegible]	---	[illegible]	231	[illegible]22	312	33[illegible]	[illegible]
[illegible]	---	2.	3.4	[illegible]	1.5	1.7	[illegible]
[illegible]	--	9.	9.0	[illegible]	10	9.[illegible]	[illegible]
[illegible]	---	3.	3.0	[illegible]	[illegible].2	2.[illegible]	[illegible]
[illegible]	---	1.	2.0	[illegible]	[illegible].2	0.[illegible]	[illegible]
[illegible]	---	1.	1.4	[illegible]	.8	0.7	[illegible]
[illegible]	--	7.[illegible]	7.6	[illegible]	[illegible].2	7.[illegible]	[illegible]
[illegible][1]							
Detritus %	.	1.8	[illegible]9		50	[illegible]	[illegible]
[illegible] %	.	5.1	.2		19	[illegible]	[illegible]
Liverwort %	.	.	1.2	.	[illegible].3	.	.
Mushroom %	.	.	.	.	.2	.	.
[illegible]	.	.	[illegible]	0.4	.9	[illegible]	[illegible]
[illegible]	.		.		.1	.	.
[illegible]	.	[illegible]	[illegible]	[illegible]	20	.	.
Bare Ground %	.	.	.	.	.	.	.
Flood-Water Duration (months)	.	[illegible]	.	.	.	.	.
Height (metres)	.	.		.	.		.
Representative Age (years)	.		.	[illegible]	.	.	.
Biomass Properties[illegible]							
[illegible]	---	---	---				
[illegible]	---	---	---	.	.	.	
[illegible]	---	---	---	[illegible]	[illegible]	[illegible]	
[illegible]	---	---	---	[illegible]			.
Shrub (kg/ha)	---	---	---	342	.		.
Total (kg/ha)	---	---	---	739	.	.	.
[illegible]							
Shrub	.	.	.		.		
B. Species Composition[1]							
[illegible]	.				.	.	.
S. bebbiana	.	.		.	.		.
Populus balsamifera	.	.	.	.		[illegible]	
Alnus tenuifolia	.	.	.	.		[illegible]	.
Picea glauca	.	.	.	.			
Betula papyrifera	.	.	.	.			.
[illegible]							
Betula papyrifera	.	.		.	.		.
Salix pseudomonticola	[illegible]						
S. interior	[illegible]						
[illegible]							
Carex atherodes	.	47			.	.	
[illegible]	.	1.0	.		.	.	.
Typha latifolia	.	36	[illegible]	.	.	.	
Lysimachia thyrsiflora	.	0.3	1.	.	.	.	.
Ranunculus gmelinii	.	0.5	.	.	.	.	.
Potentilla anserina	.	0.5	.	8.	.	.	.
Eleocharis palustris	.	0.5	.	1.	.	.	.
Sparganium angustifolium	.	0.5	.	1.	.	.	.
Rumex maritimus	.	0.5	.	0.[illegible]	.	.	.
Equisetum fluviatile	.	1.4	.	0.	.	.	
Rorippa islandica	.	6	.	1[illegible]	.	.	
Carex bebbii	.	1.5		0.	.	.	
Potentilla [illegible]	.	1.0		1.	.	.	.
Plantago major	.	0.8	.	7.	.		.
[illegible]	.	1.0	.	.	.	.	.
Epilobium angustifolium	.	0.5		8.	.	.	.
Artemisia biennis		0.5	.		.	.	.
Equisetum palustre	.	.		.	.	.	.
Mentha arvensis	.	.	.	.	.	.	.
Aster [illegible]		.	.	.	.	.	.
Equisetum arvense	.	.	.	.	.		.
Salix interior	.						.
S. [illegible]	.	.		.		.	.
Agropyron trachycaulum		.		[illegible]	.		.
Epilobium glandulosum	.	.		[illegible]	.	.	.
[illegible]		.		.		.	.
Sphenopholis obtusata	[illegible]						
[illegible]							
Populus balsamifera	[illegible]						
Alnus tenuifolia	[illegible]						
Picea glauca	[illegible]						
Salix bebbiana	[illegible]						
Equisetum pratense	[illegible]						
[illegible]							
Salix pyrifolia	[illegible]						
[illegible]							
Carex sychnocephala	[illegible]						
Juncus nodosus	[illegible]						
Puccinellia nuttalliana	[illegible]						
Hordeum jubatum	[illegible]						
Ranunculus macounii	[illegible]						
Melilotus alba	[illegible]						
[illegible]							
Juncus balticus	[illegible]						
Erigeron philadelphicus	[illegible]						
[illegible]							
Fragaria vesca	[illegible]						
[illegible]							
Fragaria virginiana	[illegible]						
Agrostis scabra	[illegible]						
[illegible]							
Poa pratensis	[illegible]						
Rubus pubescens	[illegible]						
[illegible]							
Rubus strigosus	[illegible]						
Solidago lepida	[illegible]						
[illegible]							
Viburnum edule	[illegible]						
[illegible]							
Aralia nudicaulis	[illegible]						
Cornus canadensis	[illegible]						
Linnaea borealis	[illegible]						
[illegible]							
Galium boreale	[illegible]						
Maianthemum canadense	[illegible]						
Actaea rubra	[illegible]						
Pyrola virens	[illegible]						

[illegible] Community Types: 1) Algal Aquatic, 3) Herb Immature Marsh, 10) Swale Shrub, 9) Levee Herb, 11) Levee Shrub, 12) Levee Tree, 13) Upland [illegible]

[illegible] 26, 27 September 1971.

[illegible] only in one community type and having a mean PV < 1.0 there [illegible]; see species/zone tables for complete species compositions of [illegible]

[illegible] *Scirpus microcarpus*, *Sisyrinchium* [illegible] *capitatum*, *C. leptophyllum*, *Kochia scoparia*, *Collemia* [illegible] *guttatus*, *Utricularia intermedia* not listed in the table).

effects.

Shrub Stratum (Table 33)

This stratum is found in allogenic Swale Shrub, Levee Herb, and Levee Shrub; polygenic Levee Tree; and autogenic Upland Forest CT's. The Levee Shrub CT has the highest shrub cover, resulting probably from low tree cover and relatively short periodic floods. Total shrub cover seems positively associated with height above MSWL; available soil potassium; total detritus, moss, lichen, and tree covers; and representative age, and negatively with flood-water duration; soil moisture; available water; and total water and bare ground covers. These relationships indicate that species in this stratum are likely intolerant of prolonged flooding and its effects.

Shrub biomass peaks in the Levee Shrub CT and seems positively associated with total woody detritus and liverwort covers. Shrub biomass is thus maximal in annually to periodically flooded communities.

Average shrub species richness per zone increases throughout the successional sequence, peaking in the Upland Forest CT. Environmental stress from flooding effects is an important contributor to the low species diversity of Levee Herb, Shrub, and Tree CT's. Shrub species richness seems positively associated with height above MSWL; available soil potassium; total detritus, moss, lichen, shrub, and tree covers; and representative age,

and negatively with flood-water duration; soil moisture, available water, and total water and bare ground covers. These relationships indicate that increases in shrub species diversity may reflect decreased flooding and its related effects.

Shrubs, like trees, make an important contribution to community structure along the successional gradient.

Herb-Dwarf Shrub Stratum (Table 33)

Except for the Algal Aquatic, this stratum is found in all CT's. Total herb-dwarf shrub cover peaks in the Upland Forest CT, and appears positively associated with silt; sulphate; and conductivity, and negatively with flood-water duration, and total water and bare ground covers. These relationships indicate that many herb species are intolerant of flooding and its related effects in this study area.

The major growth-form components of the bryoid and herb-dwarf shrub strata show different biomass distributions and optima in the successional sequence. Bryoid biomass increases throughout the sequence, peaking in the Upland Forest CT. It seems positively associated with PWP, and organic matter, and negatively with calcium carbonate content. Graminoid biomass is very low in this sequence, peaking in the Levee Herb CT, then decreasing upslope. Graminoids evidently do not do well in rapidly drained situations, though they can tolerate flooding.

Forb biomass shows a bimodal distribution, peaking in the Levee Herb and Upland Forest CT's. It seems positively associated with sulphate and conductivity values, and total herb-dwarf shrub cover. Dwarf shrub biomass, composed mostly of *Salix* spp., peaks in the Levee Shrub CT.

Average herb-dwarf shrub species richness per zone shows a bimodal pattern with peaks in the allogenic Swale Shrub and autogenic Upland Forest CT's. Environmental stress from flooding effects on the herb-dwarf shrub species of Levee Herb, Shrub, and Tree CT's is very strong.

Total bare ground cover appears positively associated with flood-water duration, and sand and soil moisture contents, and negatively with height above MSWL; clay and available soil potassium contents; total detritus, moss, lichen, herb, shrub, and tree covers; and representative age. These relationships suggest that higher bare-ground cover is found in low flood-prone areas subject to increased action from the hydrologic regime factors.

iii. Synthesis

Species presence and abundance patterns along the successional sequence are given in Table 33B. Species seem aligned primarily according to increasing height above MSWL and, hence, to decreasing flood-water duration

and flood frequency and their associated and residual effects. Shelter, physical and chemical soil properties, and vegetation cover also contribute to variations in species abundances in the sequence. Topographic, hydrologic, and edaphic factors appear to restrict *Salix interior* in the tree stratum, and *Scirpus microcarpus*, *Sisyrinchium montanum*, *Chenopodium capitatum*, and five other species in the herb-dwarf shrub stratum to this study area.

In more exposed sections the shrub *Salix pyrifolia*, dwarf shrubs such as *S. interior* and *S. lutea*, and herbs such as *Potentilla anserina* and *Equisetum arvense* have their optima in the allogenic Levee Herb CT. These species can tolerate most annual flooding effects, *e.g.* sedimentation, while stabilizing and promoting the build-up of this CT. With the presence of a more ameliorated terrestrial environment the tree *S. bebbiana*, shrubs such as *S. interior* and *S. lasiandra*, and herbs such as *Epilobium glandulosum* and *Juncus balticus* attain their optima in the allogenic Levee Shrub CT. These species tolerate most periodic floods while promoting additional sediment build-up. In more sheltered sections herbs such as *Carex atherodes* and *Typha latifolia* achieve their optima in the allogenic Herb Immature Marsh CT. These species are tolerant of limited annual and periodic floods. They generally reduce flooding effects, promote sedimentation, and produce litter which eventually aid in

raising the substrate above MSWL. With the introduction of a more ameliorated terrestrial environment, the sapling *S. interior*, shrubs such as *Betula papyrifera* and *S. pseudomonticola*, dwarf shrubs such as *Alnus tenuifolia* and *Picea glauca*, and herbs such as *Epilobium angustifolium* and *Equisetum palustre* attain their optima in the allogenic Swale Shrub CT. These species give way to those in the Levee Shrub CT. Species in the foregoing CT's appear to make minor changes in soil properties and to reduce wind velocity and incident radiation, permitting a more ameliorated terrestrial environment. With further increases in height and drainage, and shelter from flooding effects, trees *Populus balsamifera* and *Alnus tenuifolia*, shrubs such as *Cornus stolonifera* and *Ribes triste*, dwarf shrubs *P. balsamifera* and *Shepherdia canadensis*, and herbs such as *Equisetum pratense* and *Agrostis scabra* attain their optima in polygenic Levee Tree CT. These species contribute greatly to increased amelioration of the environment in this study area allowing the introduction of typically Upland Forest species. With the absence of flooding and its effects trees *Picea glauca* and *Betula papyrifera*, shrubs such as *Rosa acicularis* and *Viburnum edule*, dwarf shrubs such as *Ribes oxyacanthoides* and *Rosa acicularis*, and herbs such as *Fragaria vesca* and *Pyrola asarifolia* attain their optima in the autogenic Upland Forest CT. Increasing height and shelter from flooding

and its associated and residual effects are primary factors allowing succession to proceed.

To summarize, soil development, environmental stability, species diversity, structural complexity, and age generally increase throughout the successional gradient. Components of the understory biomass exhibit variable trends. The main contribution to total biomass in this study area comes from woody species.

The *Picea glauca/Rosa acicularis/Cornus canadensis* is the most highly developed community in the successional sequence in the RC study area. The average time required to reach this community is 140 years, but varies from 120 to 180 years via the shortest and longest seral pathways.

Plant succession in the RC study area is controlled by allogenic, polygenic, and autogenic factors which produce pioneer, transitional, and terminal stages at low, middle, and high relief levels, respectively. Annual floods and fluctuating water regimes tend to retain Algal Aquatic, Herb Immature Marsh, Swale Shrub, and Levee Herb and Shrub CT's in the pioneer stage. Periodic high floods keep the Levee Tree CT in the transitional stage, while the absence of flooding allows the Upland Forest CT to achieve the terminal stage. Thus, the influence of the hydrologic regime is sufficient to retard succession to an autogenically controlled climax everywhere except the highest places. However, absence of

flooding and stabilization of water-levels (*e.g.*, by man) would allow succession to proceed quickly to the terminal stage. Plant succession in this study area is very complicated because of the development of different mud-flats and channel slopes, and because of numerous islands, terraces, and ridge-swale complexes (Fig. 3).

B. Successional Sequences in the Lake Athabasca Marsh Study Area

i. Introduction

Four CT's, having 31 zones, are represented among the three sites sampled in this study area (See Fig. 3, p. 93; Pl. 2, p. 7). Islands, levees, and low alluvial wetlands are the main landforms in this area.

ii. Succession

The prevailing successional sequence along outflow channels from Lake Athabasca is shown in Figure 5. Two distinct sequences are evident in the LAM successional diagram. In the lowest and most sheltered sections of this study area, *Typha latifolia* is the initial colonizing herb species of the EPS and IPS. It is replaced in less sheltered sections by *Eleocharis palustris* and, then, *Deschampsia caespitosa* in the LPS. In more sheltered sections *T. latifolia* is replaced by *Carex retrorsa* and/or *C. aquatilis* in the IPS. These carices are followed by *Phragmites communis* and, eventually by *Carex atherodes* in the LPS.

Figure 5. Successional diagram for the Lake Athabasca Marsh study area, showing the sequence of community and soil types and the major species' replacements in the three vascular strata[a]. Refer to p. 238 for method of determining species replacements.

Legend:

Des cae: *Deschampsia caespitosa*
Ele pal: *Eleocharis palustris*

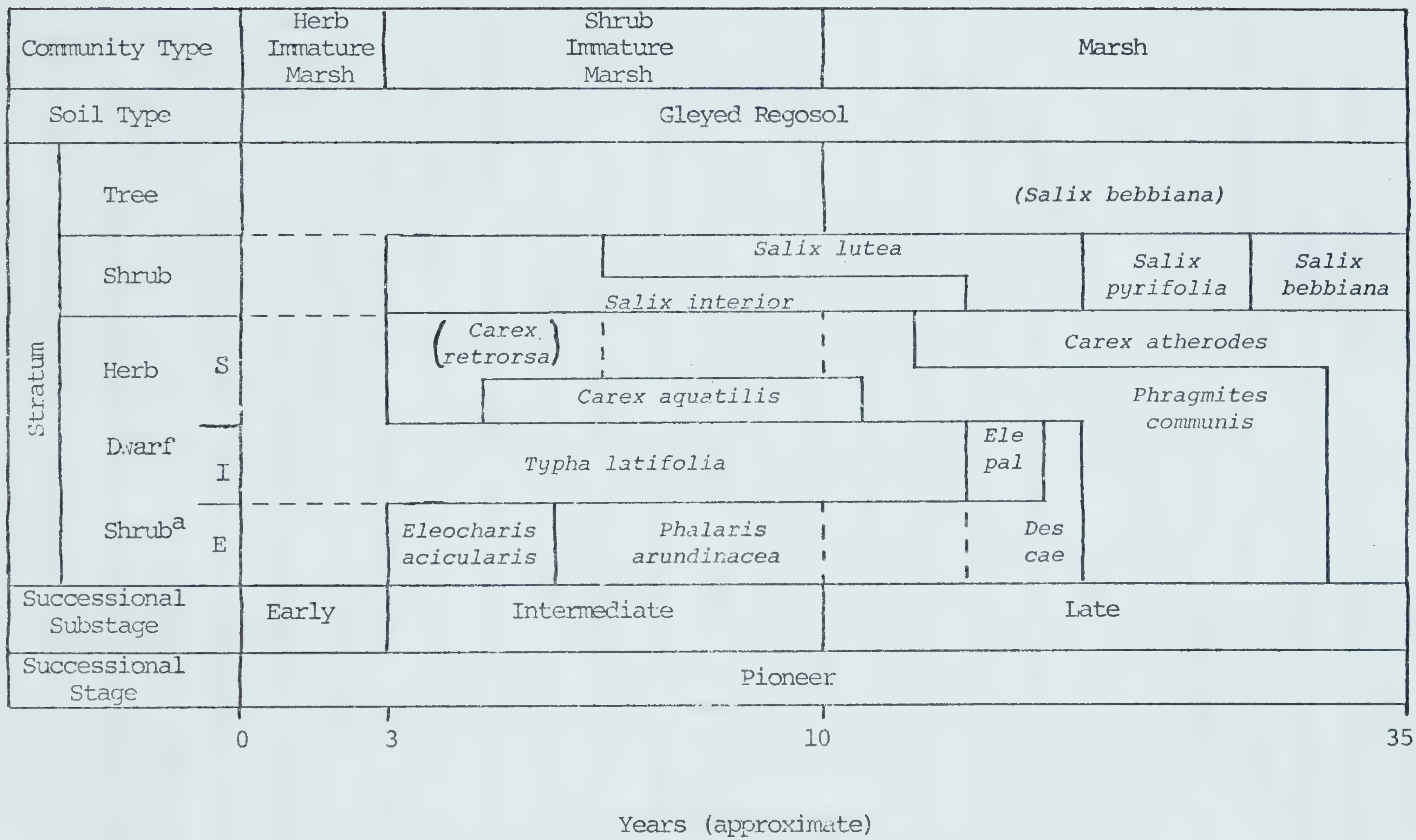
[a] Dwarf shrubs have been omitted from the herb-dwarf shrub stratum.

S: Sheltered areas.

I: Intermediate areas.

E: Exposed areas.

(): Species sometimes absent.


Community Type
Herb Immature Marsh
Shrub Immature Marsh
Marsh
Soil Type
Gleyed Regosol
Stratum
Tree
(Salix bebbiana)
Shrub
Salix lutea
Salix interior
Salix pyrifolia
Salix bebbiana
Herb
S
Carex retrorsa
Carex aquatilis
Carex atherodes
Phragmites communis
Dwarf
I
Typha latifolia
Ele pal
Shrub[a]
E
Eleocharis acicularis
Phalaris arundinacea
Des cae
Successional Substage
Early
Intermediate
Late
Successional Stage
Pioneer
0
3
10
35
Years (approximate)

In the highest and most exposed sections, *Eleocharis acicularis* is the initial colonizing herb species, followed soon after by *Phalaris arundinaceae*; both dominate the IPS. These species are replaced by *Deschampsia caespitosa*, followed by *Phragmites communis*, and later by *Carex atherodes* in the LPS.

Salix interior is the initial colonizing shrub, followed by *S. lutea*. These pioneer species are replaced by *S. pyrifolia* and later by *S. bebbiana*. The latter is the sole species in the tree stratum and occurs only in the LPS. Scattered immature individuals of *Alnus tenuifolia*, *Populus balsamifera*, *P. tremuloides*, and *Picea glauca* in the herb-dwarf shrub and shrub strata indicate possible successional trends after *S. bebbiana* if conditions of sustained drawdown were to occur.

For the herb-dwarf shrub stratum, Raup (1935:88) recognized *Eleocharis* spp. and *Carex atherodes*, *Potamogeton*, *Scirpus*, and *Calamagrostis canadensis* in his successional sequence for delta plains. *Potamogeton pectinatus* was found in this study area, but only as non-rooted stem fragments along strand-lines at the outer margins of Herb Immature Marsh and Marsh CT's. Dirschl *et al.* (1974:30) recognized *Eleocharis palustris*, *Carex* spp., and *Phragmites communis* as in Figure 5. However, he also included *Potamogeton*, *Senecio*, *Scirpus*, *Beckmannia*, *Scolochloa*, and *Calamagrostis* in his sequence.

These genera were found in the LAM study area but were nowhere dominant. Although *Phragmites communis* and *Carex atherodes* do sometimes alternate in the successional sequence, it is clear that *P. communis* is replaced eventually by *C. atherodes*. Thus the placement by Dirschl *et al.* (1974:30) of *C. atherodes* with *C. aquatilis* before *P. communis* is different.

For the shrub stratum, Raup did not recognize any species in Figure 5 as major constituents of delta plains. Both Raup and Dirschl consider *S. planifolia* as characteristic of delta plains with the latter investigator also recognizing *S. rigida* and *S. discolor*. None of these species were recorded in this or other study areas.

For the tree stratum, Raup does not indicate that *Salix bebbiana* is the major constituent of delta plains. However, Dirschl does recognize that this species is important in shrub and tree strata. Differences among sequences of this and former studies may be the result of the intensive and quantitative nature of this investigation in the northeastern portion of the PA delta.

Population analysis of tree species (Table 34) along the successional sequence indicate that environmental conditions in the EPS exclude all species. However, conditions improve marginally in the IPS. Improved drainage probably contributes to *Populus*

Table 34. Mean densities per hectare of stem size classes of major tree species in two community types along the upper segment of the successional gradient in the Lake Athabasca Marsh study area.

Tree	SC[a]	Community Type[b,c]	
		8	7
		7	*18*
Picea	sdl[d]	.	2670
glauca	trs	.	28
Populus	sdl	860	2220
balsamifera	trs	430	470
Populus	sdl	.	670
tremuloides	trs	.	390
Salix	sdl	570	3220
bebbiana	trs	.	10500
	sap	.	27
Alnus	sdl	.	440
tenuifolia	trs	.	610

a Size Class.
b Community Type: 8) Shrub Immature Marsh, 7) Marsh.
c Number of zones in the study area given in italicized numbers.
d sdl = seedlings; trs = transgressives; sap = saplings.

balsamifera apparently doing better than *Salix bebbiana*. Environmental conditions in the LPS are greatly ameliorated, allowing the appearance of *Alnus tenuifolia*, *Populus tremuloides*, and *Picea glauca*. Although these species are able to colonize, they can not sustain themselves beyond the transgressive growth form. Only *S. bebbiana* appears to do well but die-off still occurs after the sapling form is reached. Flooding effects, poor drainage, and lack of certain soil nutrients (*e.g.*, phosphorus) in sufficient quantities are limiting factors to tree growth. Kalmykov (1968) also observed that frequently flooded soils in the Neva lowland were extremely deficient in available phosphorus. Most species in this study area seem capable of withstanding flooding periods only if the water begins to recede immediately and alluviation is slight.

Tree Stratum (Table 35)

This stratum, occurring only in the LPS, is severely restricted in distribution. *Salix bebbiana*, represented only in the sapling form, is the sole species in this stratum. This species is found in the highest portion of the sequence behind strand-line deposition of large logs. This relationship suggests that this species is probably intolerant of major effects of flooding, *e.g.* sedimentation.

Table 35A. Environmental and physiognomic characteristics of community types along the successional gradient in the Lake Athabasca Marsh study area.

Table 35B. Floristic characteristics of community types along the successional gradient in the Lake Athabasca Marsh study area.

Characteristics	Community Type[a,b]			
	1	3	8	7
	5	*1*	*7*	*18*
A. Soil Physical Properties				
Soil Temperature (°C)[c]	---[d]	6.9	7.0	7.3
Sand/Clay Ratio	---	3.0	2.6	3.1
Sand %	---	60	46	50
Silt %	---	20	36	33
Clay %	---	20	18	17
Field Soil Moisture %	---	34	35	34
Field Capacity %	---	36	35	34
Permanent Wilting Point %	---	11	10	10
Available Water %	---	25	25	24
Organic Matter[e]	---	3.0	3.0	3.0
Soil Chemical Properties				
Available Phosphorus (kg/ha)	---	0.4	1.5	0.9
Available Potassium (kg/ha)	---	400	393	338
Available Nitrogen (kg/ha)	---	2.2	3.2	1.9
Calcium Carbonate[e]	---	10.0	9.7	7.8
Sodium[e]	---	3.0	3.0	2.9
Sulphate[e]	---	0.5	0.8	0.5
Conductivity (mmhos/cm)	---	0.6	0.6	0.7
pH	---	7.6	7.5	7.6
Zonal Properties[f]				
Detritus %	.	3	2	24
Woody Detritus %	.	10	2	7
Liverwort %	.	.	0.1	0.3
Mushroom %	.	.	.	0.5
Moss %	.	.	0.4	37
Herb-Dwarf Shrub %	.	38	25	61
Shrub %	.	.	20	35
Tree %	.	.	.	1.7
Bare Ground %	98	85	96	34
Water %	98	85	.	10
Flood-Water Duration (months)	6.0	3.0	3.0	2.7
Height (metres)	.	0.4	0.4	0.5
Representative Age (years)	.	3	5	21
Biomass Properties[g]				
Bryoid (kg/ha)	.	---	5	16
Graminoid (kg/ha)	.	---	173	375
Forb (kg/ha)	.	---	62	87
Dwarf Shrub (kg/ha)	.	---	43	54
Shrub (kg/ha)	.	---	108	303
Total (kg/ha)	.	---	391	835
Species Richness[h]				
Herb-Dwarf Shrub	.	6	15	31
Shrub	.	.	3	4
Tree	.	.	.	0.1
Total	.	6	16	32
B. Species Composition[i]				
Tree Stratum				
Salix bebbiana	.	.	.	8.4
Shrub Stratum				
Salix lasiandra	.	.	2.7	.
S. interior	.	.	137	143
S. lutea	.	.	56	109
S. pyrifolia	.	.	20	43
Populus balsamifera	.	.	3.9	8.3
Salix bebbiana	.	.	.	94
Alnus tenuifolia	.	.	.	10
Salix spp.	.	.	.	8.6
Populus tremuloides	.	.	.	2.8
Herb-Dwarf Shrub Stratum				
Typha latifolia	.	155	80	16
Scirpus validus	.	126	8.7	12
Sparganium angustifolium	.	23	0.7	1.1
Carex sychnocephala	.	2.0	4.9	3.5
C. atherodes	.	2.0	22	126
Equisetum fluviatile	.	2.0	0.4	2.5
Triglochin maritima	.	.	1.0	.
Eleocharis acicularis	.	.	46	7.2
Phalaris arundinacea	.	.	23	7.5
Carex retrorsa	.	.	19	3.5
Eleocharis palustris	.	.	15	14
Juncus alpinus	.	.	11	6.8
Equisetum palustre	.	.	4.9	4.1
Limosella aquatica	.	.	3.6	3.1
Senecio congestus	.	.	1.1	0.3
Rumex maritimus	.	.	0.9	0.6
Ranunculus cymbalaria	.	.	0.3	0.3
Phragmites communis ●	.	.	4.9	90
Deschampsia caespitosa	.	.	22	40
Salix interior	.	.	16	34
Calamagrostis canadensis	.	.	0.4	32
Salix lutea	.	.	4.7	32
Carex aquatilis	.	.	8.4	32
Hordeum jubatum	.	.	0.4	19
Mentha arvensis	.	.	0.9	18
Salix bebbiana	.	.	0.4	18
Beckmannia syzigachne	.	.	4.4	18
Plantago major	.	.	0.3	17
Juncus nodosus	.	.	1.1	7.1
Equisetum arvense	.	.	3.1	5.6
Rorippa islandica	.	.	0.3	5.4
Populus balsamifera	.	.	0.7	2.7
Juncus balticus	.	.	0.3	1.4
Stellaria longifolia	.	.	0.3	0.7
Solidago graminifolia ●	.	.	0.3	0.6
Juncus bufonius	.	.	0.3	0.6
Aster pansus ●	.	.	.	18
Erigeron lonchophyllus	.	.	.	18
Ranunculus macounii	.	.	.	18
Artemisia campestris ●	.	.	.	14
Poa palustris	.	.	.	13
Salix pyrifolia	.	.	.	13
Polygonum amphibium	.	.	.	13
Artemisia biennis	.	.	.	13
Vicia americana	.	.	.	11
Agrostis scabra	.	.	.	10
Sium suave	.	.	.	10
Epilobium glandulosum	.	.	.	8.0
Galium trifidum	.	.	.	7.8
Alnus tenuifolia	.	.	.	7.2
Puccinellia nuttalliana	.	.	.	6.9
Potentilla norvegica	.	.	.	5.1
Epilobium angustifolium	.	.	.	4.0
Taraxacum officinale ●	.	.	.	3.8
Scutellaria galericulata	.	.	.	2.3
Erigeron philadelphicus	.	.	.	2.3
Picea glauca	.	.	.	2.2
Polygonum aviculare ●	.	.	.	1.8
Ranunculus pensylvanicus	.	.	.	1.6
Populus tremuloides	.	.	.	1.6
Salix lasiandra	.	.	.	1.1
Carex bebbii	.	.	.	1.1
Stachys palustris	.	.	.	1.0

[a] Community Types: 1) Algal Aquatic, 3) Herb Immature Marsh, 8) Shrub Immature Marsh, 7) Marsh.
[b] Number of zones in italicized numbers.
[c] At 15 cm on 1 October 1971.
[d] No data available.
[e] Conversion scale: insignificant (0.5), L^-(2), L(3), L^+(4), M^-(5), M(6), M^+(7), H^-(8), H(9), H^+(10).
[f] Mean of % cover-class mid-points.
[g] Not including trees.
[h] Average per zone.
[i] Species recorded only in one community type and having a mean PV < 1.0 there are not listed; see species/zone tables for complete species compositions of zones.
.
● Species exclusive to this study area.

Shrub Stratum (Table 35)

This stratum is found in IPS and LPS. Its highest cover occurs in the latter stage, which has the greatest height above MSWL and lowest flood-water duration. Total shrub cover is highest in the LPS, resulting from the declining influence of flooding effects. Shrub biomass increases throughout the successional sequence, peaking in the LPS.

Average shrub species richness per zone increases throughout the sequence, peaking in the LPS. Shrub species richness appears positively associated with total shrub cover and negatively with soil clay content. Increases in shrub diversity may reflect the decreasing influence of flooding and its residual effects.

Herb-Dwarf Shrub Stratum (Table 35)

This stratum is found in all three pioneer stages. The highest cover for this stratum occurs in the LPS. Aquatic macrophytic species are notably absent. Total detritus, liverwort, mushroom, moss, and herb-dwarf shrub covers peak in the LPS. Higher bare ground cover is associated with flood-prone sections of CT's.

Growth-form components of the bryoid and herb-dwarf shrub strata increase in biomass throughout the sequence, peaking in the LPS. Forb and dwarf shrub biomasses appear positively associated with shrub species richness and height above MSWL. Graminoid biomass, however, seems

positively associated with total herb-dwarf shrub cover; total biomass; and herb-dwarf shrub and total species richness. Bryoid biomass appears positively associated with woody detritus, shrub biomass, and representative age. Thus, plant biomass and cover attain their maxima in areas not subject to the full impact of the hydrologic regime.

Average herb-dwarf shrub species richness per zone increases throughout the sequence, peaking in the LPS. It appears positively associated with total shrub cover and representative age. Thus, herb-dwarf shrub diversity is adversely affected by increases in flooding and its related effects.

iii. Synthesis

Species prominence and abundance patterns along the successional sequence are given in Table 35B. Species seem aligned primarily according to increasing height above MSWL and, hence, to decreasing flood-water duration and flood frequency and their associated and residual effects. Shelter, drainage, and physical and chemical soil properties appear to contribute to differences in species abundances in the sequence. Hydrologic and edaphic (including temperature) factors appear to restrict *Phragmites communis*, *Solidago graminifolia*, *Aster pansus*, and three other species in the herb-dwarf shrub stratum to this study area.

Certain herbs, notably *Typha latifolia*, form the first colonizing group. They attain their optima in the EPS, and can tolerate widely variable hydrologic conditions. These species reduce flood-water velocity, promote sedimentation, and produce litter, all of which eventually raise the substrate above MSWL. In a more ameliorated terrestrial environment, the shrub *Salix lasiandra* and herbs such as *Carex sychnocephala*, *Triglochin maritima*, and *Eleocharis acicularis* have their optima in the IPS. These species can tolerate most annual flooding effects while promoting the build-up of the marsh substrate. With increasing shelter from the hydrologic regime, the sapling *Salix bebbiana*, shrubs such as *S. interior* and *S. bebbiana*, dwarf shrubs such as *S. interior* and *S. pyrifolia*, and herbs such as *Carex atherodes*, *Phragmites communis*, and *Aster pansus* achieve their optima in the LPS. Although these species greatly ameliorate the marsh environment, allowing the establishment of more typically upland species, the hydrologic regime is still influential enough to prevent their maturation and, consequently, to inhibit succession.

To summarize, soil development, environment stability, species diversity, all biomass components, structural complexity, and age increase throughout the successional gradient. The main contribution to total biomass comes from graminoids and then shrubs. *Salix*

bebbiana/S. interior/Carex atherodes is the most highly developed community in the LAM successional sequence. The average time required to reach this community is *ca.* 35 years, but varies from 25 to 45 years via the shortest and longest seral pathways.

Plant succession in the LAM study area is controlled almost entirely by allogenic factors, *i.e.* the annual fluctuating flood-water regime. The influence of this regime is sufficient to prevent succession from proceeding beyond the LPS.

C. Successional Sequences in the Chilaway Snye Study Area

i. Introduction

Seven CT's, having 27 zones, are represented among the three sites sampled in this study area (See Fig. 3, p. 93; Pl. 3, p. 10). This area consists of a shallow, depositional basin partly surrounded by Precambrian outcrops.

ii. Succession

Figure 6 shows the main successional sequences in the CS basin. Two distinct sequences are evident. In both, the initial colonizing EPS species is *Potamogeton richardsonii*. In more exposed sections, it is followed by *Mentha arvensis* and, then, by *Sium suave* and *Phalaris arundinaceae*, all of which form the LPS. These species are replaced by *Carex atherodes* in the LPS and ETrS.

Figure 6. Successional diagram for the Chilaway Snye study area, showing the sequence of community and soil types and the major species' replacements in the three vascular strata[a]. Refer to p. 238 for method of determining species replacements.

Legend:

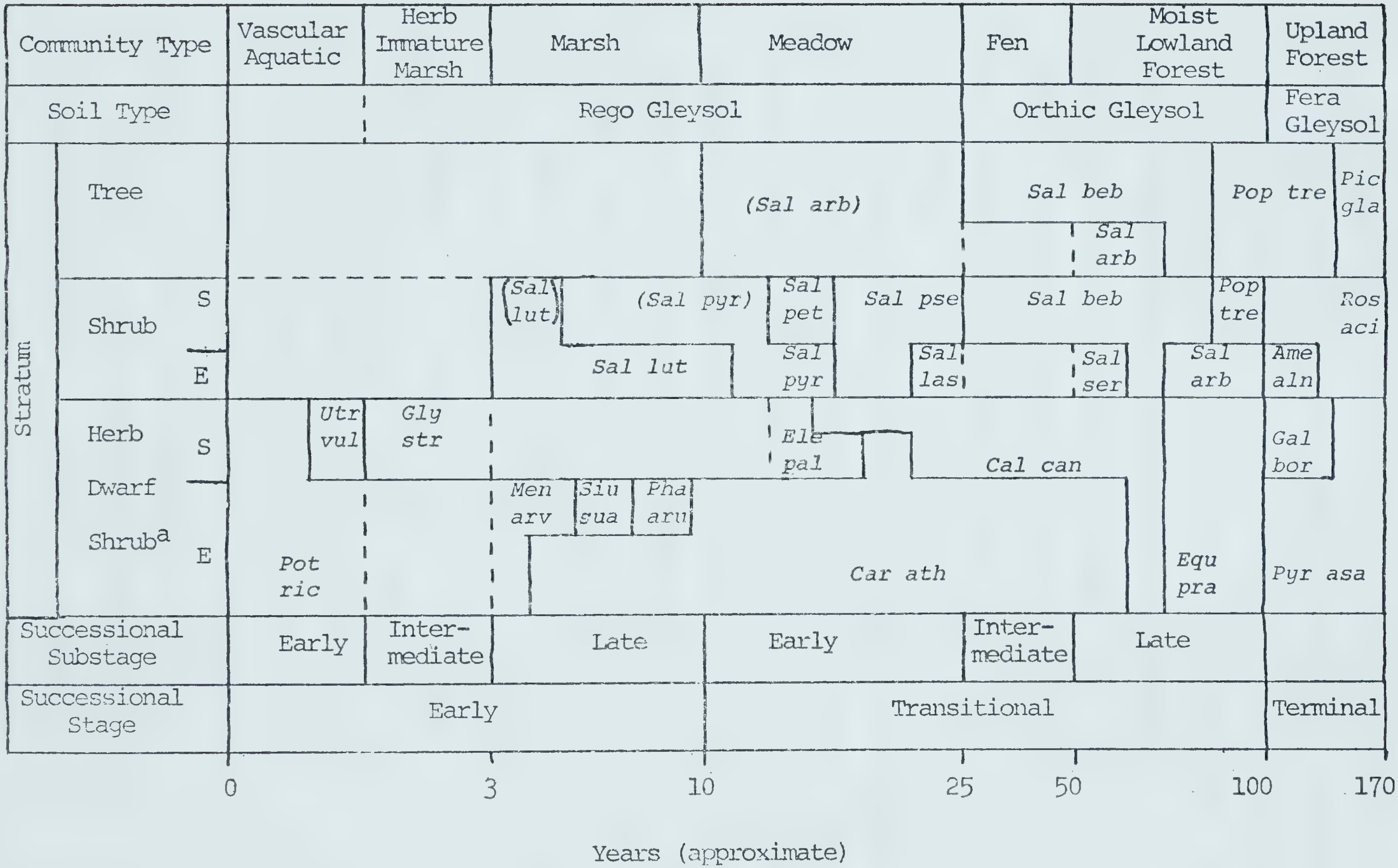
Ame aln:	*Amelanchier alnifolia*	*Pyr asa:*	*Pyrola asarifolia*
Cal can:	*Calamagrostis canadensis*	*Ros aci:*	*Rosa acicularis*
Car ath:	*Carex atherodes*	*Sal arb:*	*Salix arbusculoides*
Ele pal:	*Eleocharis palustris*	*Sal beb:*	*Salix bebbiana*
Equ pra:	*Equisetum pratense*	*Sal las:*	*Salix lasiandra*
Gal bor:	*Galium boreale*	*Sal lut:*	*Salix lutea*
Gly str:	*Glyceria striata*	*Sal pet:*	*Salix petiolaris*
Men arv:	*Mentha arvensis*	*Sal pse:*	*Salix pseudomonticola*
Pha aru:	*Phalaris arundinacea*	*Sal pyr:*	*Salix pyrifolia*
Pic gla:	*Picea glauca*	*Sal ser:*	*Salix serissima*
Pop tre:	*Populus tremuloides*	*Siu sua:*	*Sium suave*
Pot ric:	*Potamogeton richardsonii*	*Utr vul:*	*Utricularia vulgaris*

[a] Dwarf shrubs have been omitted from the herb-dwarf shrub stratum.

E: Exposed areas.

S: Sheltered areas.

(): Species sometimes absent.


Community Type
Vascular Aquatic
Herb Immature Marsh
Marsh
Meadow
Fen
Moist Lowland Forest
Upland Forest
Soil Type
Rego Gleysol
Orthic Gleysol
Fera Gleysol
Stratum
Tree
Shrub
S
E
Herb
S
Dwarf
Shrub[a]
E
(Sal arb)
Sal beb
Sal arb
Pop tre
Pic gla
(Sal lut)
(Sal pyr)
Sal pet
Sal pse
Sal beb
Pop tre
Ros aci
Sal lut
Sal pyr
Sal las
Sal ser
Sal arb
Ame aln
Utr vul
Gly str
Ele pal
Cal can
Gal bor
Men arv
Siu sua
Pha aru
Pot ric
Car ath
Equ pra
Pyr asa
Successional Substage
Early
Inter-mediate
Late
Early
Inter-mediate
Late
Successional Stage
Early
Transitional
Terminal
0
3
10
25
50
100
170
Years (approximate)

In more sheltered sections, *P. richardsonii* gives way to *Utricularia vulgaris*, both forming the EPS. *Utricularia* is then replaced by *Glyceria striata* in the IPS, followed by *Eleocharis palustris* and later by *C. atherodes* which both form the ETrS. The two latter species are replaced by *Calamagrostis canadensis* in ETrS, ITrS, and LTrS, followed by *Equisetum pratense* in the LTrS. *Equisetum* is succeeded by *Galium boreale* and/or by *Pyrola asarifolia* in the TeS.

Salix lutea is the initial colonizing shrub of the LPS. This species is followed by *S. pyrifolia* in more exposed areas of the ETrS or by *S. pyrifolia* and, then, *S. petiolaris* in more sheltered areas of the ETrS. These species are replaced by *S. pseudomonticola* in the ETrS. In less sheltered areas, this species is followed by the ETrS species, *S. lasiandra*, and later by the LTrS species, *S. serissima*, *S. bebbiana*, and *S. arbusculoides*. The latter species is replaced by *Amelanchier alnifolia* and later by *Rosa acicularis*; both dominate the TeS. *Salix bebbiana* which occurs in the ITrS and LTrS may be preceded in more sheltered areas by *S. pseudomonticola*. *Salix bebbiana* is followed by *Populus tremuloides* in the LTrS and later by *Rosa acicularis* in the TeS.

Salix arbusculoides is the initial tree species of the ETrS and is replaced by *S. bebbiana* in the ITrS and LTrS. The latter species is succeeded by *P.*

tremuloides in the LTrS and TeS, and much later by *Picea glauca*, the terminal species of the study area.

For the herb-dwarf shrub stratum, both Raup (1935:88) and Dirschl *et al.* (1974:30) recognized *Potamogeton* spp., *Glyceria* spp., *Eleocharis* spp., *Carex atherodes*, and *Calamagrostis* spp. as in Figure 6. Raup also recognized *Sparganium*, *Ranunculus*, *Myriophyllum*, *Sagittaria*, *Rorippa*, *Bidens*, *Typha*, *Equisetum fluviatile*, *Scirpus*, *Carex rostrata*, and *Beckmannia*, while Dirschl included *Nuphar*, *Senecio*, *Typha*, *Scirpus*, and *C. rostrata*. Except for *Nuphar variegatum*, *Bidens cernua*, and *Senecio congestus*, these species were also found in the CS study area but did not attain sufficient prominence to be named as part of a community by the author.

For the shrub stratum, Raup did not recognize any species in Figure 6 as major constituents in his sequence for partially ponded creeks. However, Dirschl does acknowledge *Salix bebbiana* as being important. Both Raup and Dirschl regard *Salix planifolia* as characteristic of ponded channels with the latter investigator also recognizing *S. rigida* and *S. discolor*. None of these willows were recorded in this or other study areas.

For the tree stratum, Raup recognized in his successional sequence the following two complexes:

Populus-Salix-Alnus $\longrightarrow$ *Populus-Picea* $\longrightarrow$ *Picea glauca*.

In this investigation only one complex (*Populus tremuloides-*

Betula papyrifera) has attained sufficient prominence to be named as part of a community by the author; other complexes are probably present but of much lesser prominence. *Alnus tenuifolia* was also recorded but did not attain sufficient prominence. On the other hand, Dirschl recognized the following two complexes: *Populus balsamifera-Salix bebbiana* ⟶ *P. glauca-Abies balsamea*. The latter species does not occur in the northern section of the PA delta. Neither Raup nor Dirschl mention *Betula papyrifera*. This may be the result of the extensive and non-quantitative nature of Raup's study and the more southerly location of Dirschl's study.

Population analysis of major tree species (Table 36) along the successional sequence indicates that environmental conditions in Vascular Aquatic and Herb Immature Marsh CT's exclude all species. Environmental conditions improve marginally in the Marsh CT, allowing the introduction of tree species. *Picea glauca* exhibits early mortality, but *Populus balsamifera*, *P. tremuloides*, and *Alnus tenuifolia* appear to do a little better. All species die off before reaching the sapling class. In the Meadow CT, only *Salix arbusculoides* achieves the sapling form, with remaining species dying off after the transgressive form. Only *S. bebbiana* reaches small-sized

Table 36. Mean densities per hectare of stem size classes of major tree species in five community types along the upper segment of the successional gradient in the Chilaway Snye study area.

Tree	SC[a]	Community Type[b,c]				
		7	5	6	14	13
		4	*10*	*1*	*5*	*3*
Picea	sdl[d]	2000	800	4000	4000	2670
glauca	trs	.	.	.	100	500
	sap	.	.	.	.	453
	1	.	.	.	16	427
	2	.	.	.	.	160
	3	.	.	.	.	80
	4	.	.	.	.	80
Populus	sdl	2000	.	.	.	.
balsamifera	trs	380	.	.	.	.
	sap	.	.	.	.	187
	1	.	.	.	16	160
	2	.	.	.	.	27
Populus	sdl	.	.	.	800	667
tremuloides	trs	380	50	.	1700	500
	sap	.	.	.	368	453
	1	.	.	.	384	1250
	2	.	.	.	128	267
	3	.	.	.	16	.
Salix	sdl	.	.	.	.	.
arbusculoides	trs	.	850	.	2700	.
	sap	.	8	.	240	.
Salix	sdl	.	600	4000	800	.
bebbiana	trs	.	.	29000	7300	500
	sap	.	.	3120	4880	213
	1	.	.	80	160	240
	2	.	.	.	16	53
Alnus	sdl	500	400	.	2000	.
tenuifolia	trs	250	.	.	.	.
	sap	.	.	.	.	53

[a] Size Class
[b] Community Type: 7) Marsh, 5) Meadow, 6) Fen, 14) Moist Lowland Forest, 13) Upland Forest.
[c] Number of zones in the study area given in italicized numbers.
[d] sdl = seedlings; trs = transgressives; sap = saplings; and tree dbh classes: 1 = 8-13, 2 = 13-18, 3 = 18-23, 4 = 23-28 cm.

trees, while all other species except *P. glauca* are absent as seedlings in the Fen CT. Hydrologic conditions; wet, compact, poorly aerated soil; and high herbaceous cover severely restrict the growth of most species with the probable exception of *S. bebbiana* in these CT's. *Populus tremuloides* attains its best growth in the Moist Lowland Forest CT with *Salix bebbiana* and *Picea glauca* doing much better here. *Picea glauca*, *S. bebbiana*, *P. balsamifera*, and *A. tenuifolia* grow best in the Upland Forest CT, but *P. glauca* is the only tree species showing sustained growth and an ability to self-perpetuate. The absence of any trees beyond dbh class 4 may be indicative of poor nutrient availability and of the shallow soil covering granitic outcrops in the Upland Forest CT.

Tree Stratum (Table 37)

This stratum is found in polygenic Meadow, Fen, and Moist Lowland Forest and in autogenic Upland Forest CT's, with the highest cover occurring in the latter type. Total tree cover appears positively associated with height above MSWL, and total detritus and lichen covers, and negatively with flood-water duration and soil moisture, FC, PWP, and available potassium and conductivity values.

Average tree species richness per zone increases throughout the successional sequence, peaking in the Upland Forest CT and appears positively associated with

Table 37A. [illegible] and physiognomic characteristics of community types along the successional gradient in the Chilaway Snye study area.

Table 37B. Floristic characteristics of community typ[illegible] gradient in the Chilaway Snye study area.

			4	10			3
[illegible]						4.4	
[illegible]			1.			1.4	
[illegible]						51	
[illegible]						12	
[illegible]	---						
[illegible]			37				14
[illegible]	---		39			2	20
[illegible]	---		26			7	4
[illegible]	---		19			5	16
[illegible]	---	4.0	3.0		--	.8	3.2
[illegible]	---	5.6	4.2		--	8	44
[illegible]	---	525	5.6		---		284
[illegible]	---	5.6	1.1		---		0.4
[illegible]	---	0.5	2.6		-		3.7
[illegible]	---	4.0	3.2		--		3.0
[illegible]	---	8.0	.5				0.5
[illegible]	---	2.7	.6		--		0.3
[illegible]	---	7.2	.4				7.5
[illegible]			8			8	
[illegible]			1				
[illegible]						0.2	
[illegible]						8	
[illegible]						1	
[illegible]						4	
[illegible]						5	
Water %	98						
Flood-Water Duration (months)	6.0					1.	
Height (metres)						1.1	
Representative Age (years)							
Biomass Properties							
Bryoid (kg/ha)		---			-		
[illegible]		---			---	40	
[illegible]		---			---		
[illegible]		---			---	0.	
Shrub (kg/ha)		---			---	43	
[illegible]		---			---	64	
Species Richness							
[illegible]						1	
Tree							
Species Composition						1	
S. bebbiana							
Picea glauca							
Alnus tenuifolia							
Shrub Stratum							
Populus balsamifera							
Salix lutea							
S. pyrifolia							
Betula papyrifera							
S. lasiandra							
S. arbusculoides							
Typha latifolia							
Carex atherodes							
Plantago major							
Carex bebbii							
Phleum pratense							
Chenopodium album							
Salix lutea							
Salix pyrifolia							
Deschampsia caespitosa							
Hippuris vulgaris							
Juncus bufonius							
Rorippa islandica							
Salix petiolaris							
Epilobium glandulosum							
Mentha arvensis							
Betula papyrifera							
Alnus tenuifolia							
Sium suave							
Poa palustris							
Equisetum fluviatile							
Erigeron philadelphicus							
Geum aleppicum							
Equisetum pratense							
Aster puniceus							
Poa pratensis							
Sphenopholis obtusata							
Agrostis scabra							
Epilobium angustifolium							
Populus tremuloides							
Solidago lepida							
Linnaea borealis							
Viburnum edule							
Rosa acicularis							
Rubus strigosus							
Aralia nudicaulis							
Poa interior							

Community Type: 2) Vascular Aquatic, 1[illegible] marsh, [illegible] 5) Meadow, 6) Fen, 14) [illegible] forest, [illegible] forest.

Number of zones given in [illegible].

At 15 cm level on 30 September [illegible].

Conversion scale: insignificant [illegible] H-(8), H(9), H+(10).

Mean of % cover-class mid-points.

[illegible] including trees.

height above MSWL; total lichen and tree covers; and representative age, and negatively with flood-water duration; and soil moisture, FC, and PWP contents. These relationships suggest that increases in tree diversity, like total tree cover, may reflect decreasing influence of periodic flooding and its residual effects.

Shrub Stratum (Table 37)

This stratum is found in allogenic Marsh; polygenic Meadow, Fen, and Moist Lowland Forest; and autogenic Upland Forest CT's. The latter type has the highest shrub cover, resulting probably from the lack of flooding. Total shrub cover appears positively associated with total detritus and mushroom covers, and negatively with flood-water duration, soil temperature, and total bare ground cover. These relationships indicate that most shrub species are intolerant of prolonged flooding and its related effects.

Shrub biomass increases throughout the successional sequence, peaking in the Upland Forest CT and seems positively associated with total mushroom and shrub covers. Shrub biomass is thus maximal in non-flooded communities.

Average shrub species richness per zone generally increases throughout the successional sequence, peaking in the Upland Forest CT. Shrub species richness appears positively associated with height above MSWL and various

species of different strata. These relationships indicate that increases in shrub diversity may reflect decreasing influence of flooding and its residual effects and increasing vegetation cover in shrub and tree strata. Environmental stress from periodic flooding effects is important in contributing to low species diversity in certain polygenic types.

Herb-Dwarf Shrub Stratum (Table 37)

This stratum is found in all CT's, with the highest cover occurring in the Meadow Type.

Growth-form components of the bryoid and herb-dwarf shrub strata show variable biomass trends along the successional sequence. While shrub biomass increases throughout the sequence, forb and dwarf shrub biomasses show bimodal patterns with peaks in the Meadow and Upland Forest CT's. Bryoid biomass also exhibits a bimodal pattern with peaks in the Marsh and Upland Forest CT's. Graminoid biomass peaks in the Meadow CT.

Average herb-dwarf shrub species richness per zone shows a bimodal pattern with peaks in the allogenic Marsh and autogenic Upland Forest CT's. Environmental stress from periodic flooding effects on the herb-dwarf shrub species of the Moist Lowland Forest CT is sufficient to cause the reduction of diversity to those flood-tolerant species only capable of completely adapting to increased shade. A decrease in topographic variation

(hummock-hollow complexes) from Fen to Moist Lowland CT's also probably contributes to declining herb-dwarf shrub diversities in these types. High species diversity in the Marsh CT probably reflects the transition between aquatic and terrestrial environments.

Total bare ground cover appears positively associated with flood-water duration; soil temperature; available water and sulphate contents, and negatively with total detritus, mushroom, and shrub covers. These relationships suggest that higher bare ground cover is found in low flood-prone areas.

iii. Synthesis

Species presence and abundance patterns along the successional sequence are given in Table 37B. Species seemed aligned primarily according to increasing height above MSWL and decreasing flood-water duration and flood frequency and their associated and residual effects. Shelter, drainage, and physical and chemical soil properties seem to contribute to differences in species abundances in the sequence. Topographic, physiographic, and hydrologic factors seem to restrict *Salix scouleriana* in the tree stratum, and *Potamogeton gramineus*, *P. pusillus*, *Glyceria striata*, and eight other species in the herb-dwarf shrub stratum to this study area.

Herbs such as *Potamogeton richardsonii* and *Utricularia vulgaris* have their optima in the Vascular

Aquatic CT and help stabilize this type, allowing species of the next stage to colonize. In more sheltered areas, herbs such as *Glyceria striata*, *Sparganium angustifolium*, *Eleocharis acicularis*, and *Scirpus validus* attain their optima in the Herb Immature Marsh CT, and promote additional sediment build-up. In more exposed areas, shrubs such as *Alnus tenuifolia* and *Salix lutea*, dwarf shrubs such as *Salix lutea*, *Alnus tenuifolia* and *Populus balsamifera*, and herbs such as *Carex sychnocephala*, *Phalaris arundinacea*, *Mentha arvensis*, and *Poa palustris* attain their optima in the Marsh CT. These species promote additional sediment build-up and help stabilize the substrate. With a more ameliorated environment, shrubs such as *S. petiolaris* and *S. pseudomonticola*, the dwarf shrub *S. bebbiana*, and herbs such as *Typha latifolia*, *Carex atherodes*, *Ranunculus pensylvanicus*, *Sium suave*, and *Equisetum fluviatile* attain their optima in the Meadow CT. These species tolerate most flooding effects, reduce flood-water velocity, promote sedimentation, and produce litter which eventually raises the substrate above MSWL. The shrub *Salix bebbiana* and herbs such as *Calamagrostis canadensis*, *Epilobium glandulosum*, *Potentilla norvegica*, and *Aster puniceus* have their optima in the polygenic Fen CT. These species and those from previous CT's apparently make minor changes in soil properties and reduce wind velocity and incident radiation,

permitting a more ameliorated terrestrial environment. With further increases in height above MSWL, drainage, and shelter from flooding effects trees *Salix arbusculoides*, *S. bebbiana*, and *S. scouleriana*, shrubs such as *Populus tremuloides*, *S. serissima*, and *S. scouleriana* and the dwarf shrub *Picea glauca*, and herbs such as *Equisetum pratense* and *Poa pratensis* achieve their optima in the polygenic Moist Lowland Forest CT. These species contribute greatly to increased amelioration of the environment allowing the introduction of typically Upland Forest species. With the absence of flooding and its related effects, trees such as *Picea glauca* and *Betula papyrifera*, shrubs such as *B. papyrifera*, *P. glauca*, and *Amelanchier alnifolia*, dwarf shrubs such as *Cornus stolonifera* and *Viburnum edule*, and herbs such as *Pyrola asarifolia* and *Linneae borealis* attain their optima in the autogenic Upland Forest CT. Increasing height above MSWL and shelter from flooding and its associated and residual effects are primary factors allowing succession to proceed.

To summarize, soil development, environmental stability, and age generally increase throughout the successional gradient. Components of the understory biomass exhibit variable trends. Graminoids are the main contributors to total biomass in the study area. Of the biomass components, only forbs peak in the autogenic

Upland Forest CT. Species in herb-dwarf shrub and shrub strata appear to be major contributors to total species richness. Species richness components generally tend to increase with height above MSWL and decrease with flooding and its related effects. Species diversity in the Marsh CT is higher than in adjacent CT's because of the aquatic-terrestrial transition. On the other hand, total species diversity in the Moist Lowland Forest CT is generally lower than in adjacent CT's as a result of localized stress caused by periodic flooding and its related effects.

Picea glauca/Rosa acicularis/Pyrola asarifolia is the most highly developed and stable community in the CS study area. The average time required to reach this community is *ca.* 170 years, but varies from 110 to 210 years via the shortest and longest seral pathways.

Annual fluctuating flood-water regimes tend to maintain Vascular Aquatic, Herb Immature Marsh, and Marsh CT's in the PS. Infrequently high flood-water regimes and subsequent drawdowns retain Meadow, Fen, and Moist Lowland Forest CT's in the TrS. The absence of flooding in higher places permits the climax upland forest type to develop. The hydrologic regime of lower places retards succession to the TeS. If flooding ceased and water levels stabilized in this study area, succession would proceed quickly to the TeS.

D. Successional Sequences in the Egg Lake Study Area

i. Introduction

Five CT's, having 28 zones, are represented among the three sites sampled in this study area (See Fig. 3, p. 93; Pl. 4, p. 12). This area consists of a shallow and essentially flat back-water lake basin.

ii. Succession

Figure 7 shows the main successional sequences in the EL basin. *Utricularia vulgaris* is the initial colonizing herb in the PS and is replaced, in turn, by *Lemna trisulca*, *Rorippa islandica*, the species complex (*Bidens cernua-Rumex maritimus-Carex sychnocephala*), *Scolochloa festucacea*, and *Glyceria grandis*. These species are common to the ETrS. *Carex atherodes* follows the species complex in the ETrS and *G. grandis* in the ITrS, and is replaced later by *Calamagrostis canadensis* in the LTrS and TeS. *Calamagrostis* is replaced by *Equisetum pratense* and/or *Cornus canadensis* in the TeS.

Salix petiolaris is the initial colonizing shrub of the ETrS, followed by *S. pyrifolia* in the LTrS. This species is succeeded by *S. bebbiana* which is found in the LTrS and TeS, and by *Cornus stolonifera*, *Rosa acicularis*, and *Viburnum edule* in the TeS.

Salix bebbiana is the initial colonizing tree of the TrS and TeS. This species is succeeded by *Populus balsamifera* which is in the TeS. Observations in this study area reveal that the latter species is succeeded by

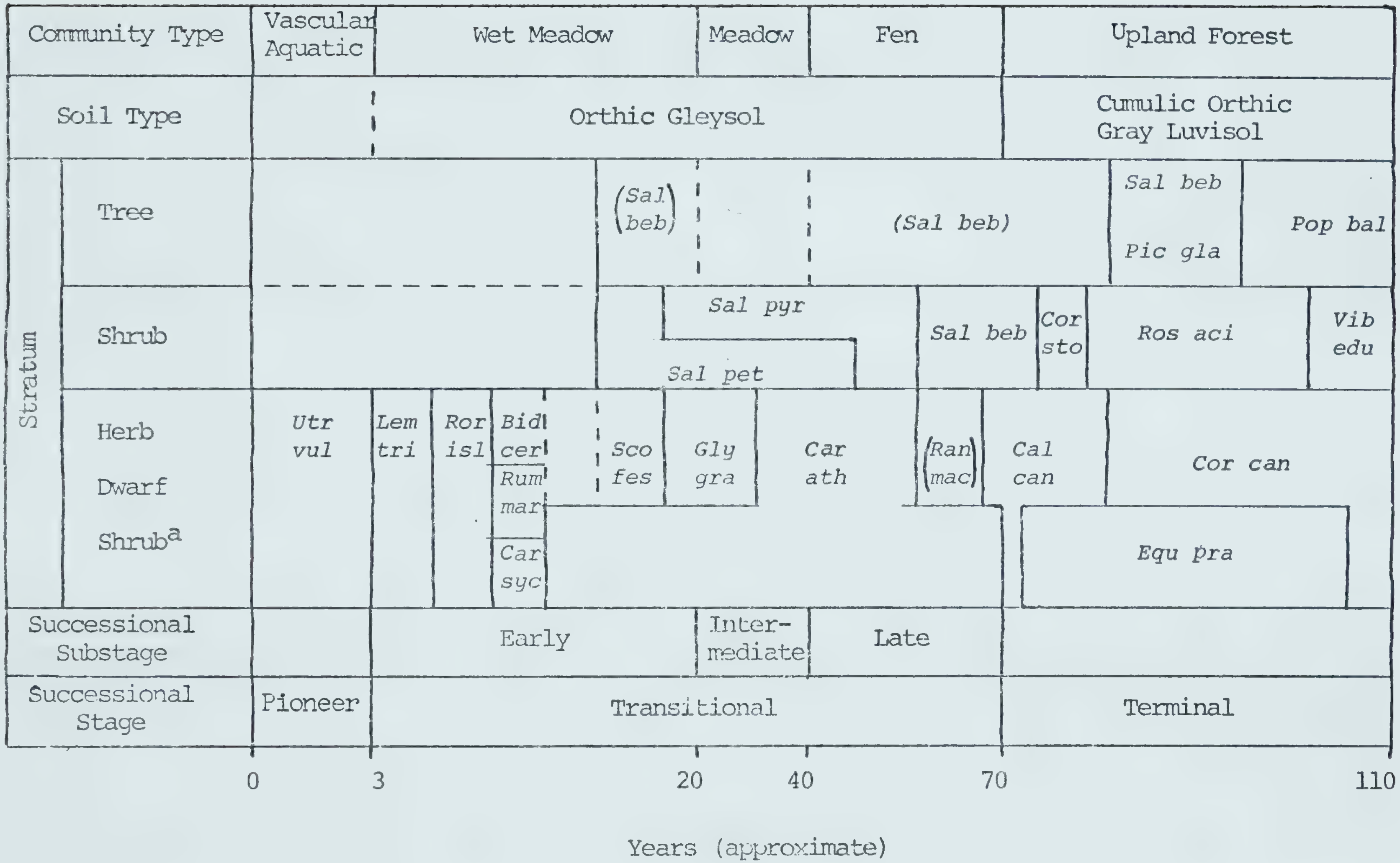
Figure 7. Successional diagram for the Egg Lake study area, showing the sequence of community and soil types and the major species' replacements in the three vascular strata[a]. Refer to p. 238 for method of determining species replacements.

Legend:

Bid cer: *Bidens cernua*
Cal can: *Calamagrostis canadensis*
Car ath: *Carex atherodes*
Car syc: *Carex sychnocephala*
Cor can: *Cornus canadensis*
Cor sto: *Cornus stolonifera*
Equ pra: *Equisetum pratense*
Gly gra: *Glyceria grandis*
Lem tri: *Lemna trisulca*
Pic gla: *Picea glauca*
Pop bal: *Populus balsamifera*
Ran mac: *Ranunculus macounii*
Ror isl: *Rorippa islandica*
Ros aci: *Rosa acicularis*
Rum mar: *Rumex maritimus*
Sal beb: *Salix bebbiana*
Sal pet: *Salix petiolaris*
Sal pyr: *Salix pyrifolia*
Sco fes: *Scolochloa festucacea*
Utr vul: *Utricularia vulgaris*
Vib edu: *Viburnum edule*

[a] Dwarf shrubs have been omitted from the herb-dwarf shrub stratum.

(): Species sometimes absent.



Community Type
Vascular Aquatic
Wet Meadow
Meadow
Fen
Upland Forest
Soil Type
Orthic Gleysol
Cumulic Orthic Gray Luvisol
Stratum
Tree
Shrub
Herb
Dwarf
Shrub[a]
(Sal beb)
(Sal beb)
Sal beb
Pic gla
Pop bal
Sal pyr
Sal pet
Sal beb
Cor sto
Ros aci
Vib edu
Utr vul
Lem tri
Ror isl
Bid cer
Rum mar
Car syc
Sco fes
Gly gra
Car ath
(Ran mac)
Cal can
Cor can
Equ pra
Successional Substage
Early
Inter-mediate
Late
Successional Stage
Pioneer
Transitional
Terminal
0
3
20
40
70
110
Years (approximate)

Populus tremuloides and later by *P. glauca*. The latter species is considered the terminal species for this study area.

For the herb-dwarf shrub stratum, Raup (1935:88) recognized only *Rorippa*, *Bidens*, *Glyceria*, *Carex atherodes*, *Ranunculus*, and *Calamagrostis* as in Figure 7. However, he also included *Potamogeton*, *Myriophyllum*, *Sagittaria*, *Typha*, *Eleocharis*, *Scirpus*, *Carex rostrata*, and *Beckmannia* in his successional sequence for ponded creeks. Dirschl *et al.* (1974:30) recognized only *Glyceria*, *C. atherodes*, and *Calamagrostis* as in Figure 7. However, Dirschl also included *Potamogeton*, *Nuphar*, *Senecio*, *Typha*, *Scirpus*, *Eleocharis palustris*, and *Carex rostrata* in his sequence for ponded channels and perched basins. Except for *Nuphar* and *Senecio*, genera mentioned by both investigators were also found in the study area but did not attain sufficient prominence to be named as part of a community by the author.

For the shrub stratum, Raup did not recognize any species in Figure 7 as major constituents of ponded creeks. However, Dirschl does acknowledge that *S. bebbiana* is important. Both Raup and Dirschl acknowledge that *S. planifolia* is characteristic of backwater areas with the latter investigator also recognizing *S. rigida* and *S. discolor*. None of these species were recorded in this or other study areas.

For the tree stratum, Raup recognized two complexes in his sequence: *Populus-Salix-Alnus* ⟶ *Populus-Picea* ⟶ *P. glauca*. In this investigation only one complex (*S. bebbiana-P. glauca*) has attained sufficient prominence to be named as part of a community by the author; other complexes are probably present but of much lesser prominence. On the other hand, Dirschl only recognized the following two complexes in his sequence: *Populus balsamifera-Salix bebbiana* ⟶ *P. glauca-Abies balsamea*. Except for the latter species which does not occur in the study region, all species mentioned by Raup and Dirschl are present in this study area. Differences among sequences of this and former studies may be the result of the intensive and quantitative nature of this investigation in the northeastern portion of the PA delta.

Population analysis of major tree species (Table 38) along the successional sequence indicates that environmental conditions in the Vascular Aquatic CT exclude all species. However, conditions for trees improve in the Wet Meadow and Meadow CT's, allowing the introduction of *Salix bebbiana* and *Picea glauca* respectively. In the Fen CT, only *S. bebbiana* is able to reach small-sized trees as *P. glauca*, *Populus balsamifera*, and *Alnus tenuifolia* die-off before reaching the sapling form. In the Upland Forest CT, *Populus tremuloides* and *S. arbusculoides* are introduced, and all species reveal

Table 38. Mean densities per hectare of stem size classes of major tree species in four community types along the upper segment of the successional gradient in the Egg Lake study area.

Tree	SC[a]	Community Type[b,c]			
		4	5	6	13
		9	*3*	*7*	*5*
Picea glauca	sdl[d]	.	2000	290	1200
	trs	.	.	.	100
	sap	.	.	.	48
	1	.	.	.	64
	2	.	.	.	16
Populus balsamifera	sdl	.	.	860	400
	trs	.	.	.	300
	sap	.	.	.	181
	1	.	.	.	256
	2	.	.	.	112
	3	.	.	.	160
	4	.	.	.	32
	5	.	.	.	16
	6	.	.	.	.
	7	.	.	.	.
	8	.	.	.	16
Populus tremuloides	sdl	.	.	.	.
	trs	.	.	.	.
	sap	.	.	.	32
	1	.	.	.	16
	2	.	.	.	16
	3	.	.	.	.
	4	.	.	.	16
Salix arbusculoides	sdl	.	.	.	.
	trs	.	.	.	300
	sap	.	.	.	128
	1	.	.	.	48
Salix bebbiana	sdl	.	.	3710	.
	trs	.	.	13710	1100
	sap	9	.	4220	1070
	1	.	.	11	304
	2	.	.	.	144
	3	.	.	.	64
Alnus tenuifolia	sdl	.	.	.	1200
	trs	.	.	71	800
	sap	.	.	.	64

[a] Size Class

[b] Community Type: 4) Wet Meadow, 5) Meadow, 6) Fen, 13) Upland Forest.

[c] Number of zones in the study area given in italicized numbers.

[d] sdl = seedlings; trs = transgressives; sap = saplings; and tree dbh classes: 1 = 8-13, 2 = 13-18, 3 = 18=23, 4 = 23-28, 5 = 28-33, 6 = 33-38, 7 = 38-43, 8 = 43-48 cm.

their best growth. Previous periodic flooding effects probably account for the absence of *P. glauca* and *P. tremuloides* at dbh class 3, and the elimination of *P. tremuloides* and decline of *P. balsamifera* at dbh class 5. Absence of dbh classes 6,7 in the population pattern of *P. balsamifera* may be the indirect result of the hydrologic regime. Environmental conditions, such as abundant soil moisture, inadequate drainage, and periodic flooding influences, appear to prevent *P. tremuloides* and *P. glauca* from achieving higher dbh classes. In addition to the presence of unsuitable seed beds, similar factors probably prevent these species from successfully succeeding *P. balsamifera* until more ameliorated environments of levee crests of the RC study area are approached.

Tree Stratum (Table 39)

This stratum is found in polygenic Wet Meadow and Fen; and autogenic Upland Forest CT's, with the highest cover occurring in the latter type. Total tree cover appears positively associated with height above MSWL, total available phosphorus content, and total woody detritus and shrub covers, and negatively with water duration, and available water and sodium contents. These relationships indicate that tree species are very intolerant of flooding and its effects and of high soil moisture.

Average tree species richness per zone increases

Table 40A. [illegible]ental and physiognomic characteristics of community types along the successional gradient in the Egg Lake study area.

[illegible] gradient in the Egg Lake study area.

	Community Type[a,b]				
	3	4	5	6	7
[illegible]					
[illegible]	---[1]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	---	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	---	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	---	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	---	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] Soil Moisture %	---	1	[illegible]	[illegible]	[illegible]
[illegible]	---	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	---	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	---	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	---	1	[illegible]	[illegible]	[illegible]
[illegible]	---	.3	---	[illegible]	[illegible]
[illegible] Properties					
Available Phosphorus (kg/ha)	---	5.2	--	[illegible]	[illegible]
Available Potassium (kg/ha)	---	206	---	[illegible]	[illegible]
[illegible]	---	1.[illegible]	---	[illegible]	[illegible]
[illegible] Carbonate	--	0.[illegible]	---	[illegible]	[illegible]
[illegible]	---	4.[illegible]	--	[illegible]	[illegible]
[illegible]	---	0.[illegible]	---	[illegible]	[illegible]
[illegible]	---	0.[illegible]	---	[illegible]	[illegible]
[illegible]	---	7.[illegible]	---	[illegible]	[illegible]
[illegible]					
[illegible]	.	6[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	.	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	.	0.1	.	.	.
[illegible]	.	0.1	[illegible]	[illegible]	[illegible]
[illegible]	.	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	.	.	.	.	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	.	[illegible]	[illegible]	[illegible]	[illegible]
Bare Ground %	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Water %	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	.	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]					
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	.	[illegible]	---	[illegible]	[illegible]
[illegible]	.	[illegible]	---	[illegible]	[illegible]
Forb (kg/ha)	[illegible]	[illegible]	---	[illegible]	[illegible]
Dwarf Shrub (kg/ha)	[illegible]	[illegible]	---	[illegible]	[illegible]
[illegible]	.	.	---	.	[illegible]
[illegible]	.	.	---	.	[illegible]
[illegible]	[illegible]	[illegible]	---	[illegible]	[illegible]
[illegible]					
Herb-Dwarf Shrub	.	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	.	[illegible]	[illegible]	[illegible]	[illegible]
Tree	.	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	.	[illegible]	[illegible]	[illegible]	[illegible]
Species Composition[1]					
[illegible]					
Salix bebbiana	.	[illegible]	.	.	[illegible]
Populus balsamifera	.	.	.	.	[illegible]
Picea glauca	.	.	.	.	[illegible]
Betula papyrifera	.	.	.	.	[illegible]
Salix arbusculoides	.	.	.	.	[illegible]
Alnus tenuifolia	.	.	.	.	[illegible]
Populus tremuloides	.	.	.	.	[illegible]
Shrub Stratum					
Salix pseudomonticola	.	[illegible]	[illegible]	.	.
S. petiolaris	.	[illegible]	11	[illegible]	.
S. pyrifolia	.	[illegible]	.	[illegible]	.
S. [illegible]	.	[illegible]	.	.	.
S. glauca	.	.	.	[illegible]	.
Salix bebbiana	.	.	.	[illegible]	[illegible]
Rosa acicularis	.	.	.	[illegible]	[illegible]
[illegible]	.	.	.	[illegible]	[illegible]
Alnus tenuifolia	.	.	.	[illegible]	[illegible]
[illegible]	.	.	.	.	[illegible]
[illegible]	.	.	.	.	[illegible]
[illegible]	.	.	.	.	[illegible]
[illegible]	.	.	.	.	[illegible]
[illegible]	.	.	.	.	[illegible]
[illegible]	.	.	.	.	[illegible]
[illegible]	.	.	.	.	[illegible]
[illegible]	.	.	.	.	[illegible]
[illegible]	[illegible]	.	.	.	.
[illegible]	[illegible]	.	.	.	.
[illegible]	[illegible]	.	.	.	.
[illegible]	[illegible]	.	.	.	.
[illegible]	.	[illegible]	.	.	.
[illegible] *	[illegible]	[illegible]	.	.	.
Sparganium angustifolium	[illegible]	[illegible]	.	.	.
Alisma plantago-aquatica	.	[illegible]	.	.	.
[illegible]	.	1	.	.	.
Ceratophyllum demersum	.	.	.	.	.
[illegible]	.	.	[illegible]	[illegible]	.
Bidens cernua	.	.	.	.	.
Rumex maritimus	.	[illegible]	.	.	.
[illegible]	.	[illegible]	.	.	.
Typha latifolia	.	[illegible]	.	.	.
[illegible]	.	.	.	.	.
Juncus bufonius	.	[illegible]	.	.	.
[illegible] *	.	.	.	.	.
Ranunculus aquatilis *	.	.	.	.	.
[illegible]	.	.	.	[illegible]	.
Rorippa islandica	.	[illegible]	[illegible]	[illegible]	.
[illegible]	.	[illegible]	[illegible]	[illegible]	.
Salix petiolaris	.	.	[illegible]	[illegible]	.
Ranunculus natans *	.	[illegible]	.	[illegible]	.
Polygonum amphibium	.	[illegible]	.	13	.
[illegible]	.	[illegible]	.	[illegible]	.
[illegible]	.	.	.	[illegible]	.
[illegible] *	.	[illegible]	.	[illegible]	.
[illegible]	.	.	.	13	.
[illegible]	.	.	.	[illegible]	.
[illegible]	.	.	.	.	.
[illegible]	.	.	.	.	.
[illegible]	.	.	.	.	.
[illegible]	.	.	.	.	.
[illegible]	.	.	.	.	.
Mentha arvensis	.	.	1.[illegible]	.	.
Erigeron philadelphicus	.	.	1.0	.	.
Sium suave	.	.	[illegible]	.	.
[illegible]	.	.	16	.	.
[illegible]	.	.	.	.	.
[illegible]	.	.	.	[illegible]	.
[illegible] *	.	.	.	[illegible]	.
[illegible]	.	.	[illegible]	.	.
[illegible]	.	.	.	[illegible]	.
Geum allepicum	.	.	.	.	.
Polygonum lapathifolium	.	.	.	.	.
Salix bebbiana	.	.	.	8.[illegible]	.
[illegible]	.	.	.	[illegible]	[illegible]
[illegible]	.	.	.	[illegible]	[illegible]
Ribes hudsonianum	.	.	.	3.[illegible]	.
[illegible]	.	.	.	0.[illegible]	.
[illegible]	.	.	.	0.[illegible]	.
[illegible]	.	.	.	0.[illegible]	.
[illegible] *	.	.	.	3.[illegible]	.
[illegible]	.	.	.	1.[illegible]	.
Actaea rubra	.	.	.	0.[illegible]	[illegible]
[illegible]	.	.	.	[illegible]	.
[illegible]	.	.	.	2.3	.
[illegible] *	.	.	.	0.6	.
Rumex mexicanus *	.	.	.	0.3	.
[illegible]	.	.	.	0.3	.
Rubus pubescens	.	.	.	1	.
[illegible]	.	.	.	.	.
Rosa acicularis	.	.	.	.	.
[illegible]	.	.	.	.	.
[illegible]	.	.	.	.	[illegible]
[illegible]	.	.	.	.	.
[illegible]	.	.	.	.	.
Rubus strigosus	.	.	.	.	[illegible]
[illegible]	.	.	.	.	.
[illegible]	.	.	.	.	[illegible]
Pyrola asarifolia	.	.	.	.	.
Lathyrus ochroleucus	.	.	.	.	.
Mitella nuda	.	.	.	.	.
[illegible]	.	.	.	.	[illegible]
[illegible]	.	.	.	.	.
[illegible]	.	.	.	.	1.[illegible]
[illegible]	.	.	.	.	1.[illegible]
[illegible]	.	.	.	.	1.[illegible]
Solidago lepida	.	.	.	.	[illegible]
[illegible]	.	.	.	.	.
[illegible]	.	.	.	.	[illegible]

[illegible] Vascular Aquatic, 4) Wet Meadow, 5) Meadow, 6) Fen, [illegible] Forest.
[illegible]es given in italicized numbers.
[illegible]el on 28 September 1971.
[illegible]
[illegible] 0).
[illegible] class mid-points.
[illegible]
[illegible] per zone.
[illegible] recorded only in one community type and having a mean PV < 1.0 there [illegible] listed; see species/zone tables for complete species composition of [illegible].
* [illegible] *Ranunculus pedatifidus*, *Thalictrum venulosum*, *Sonchus [illegible]* is not listed in the table).

throughout the successional sequence, peaking in the Upland Forest CT and appears positively associated with height above MSWL; available phosphorus content; total woody detritus and tree covers, and representative age, and negatively with water duration and sodium content. These relationships suggest that increases in tree species diversity may reflect decreased periodic flooding and its residual effects.

Shrub Stratum (Table 39)

This stratum is found in polygenic Wet Meadow, Meadow, and Fen; and autogenic Upland Forest CT's, with the highest cover occurring in the latter type. Total shrub cover appears positively associated with total tree cover and negatively with available water and PWP contents. These relationships indicate that shrub species are generally intolerant of flooding and its related effects and of high soil moisture.

Shrub biomass peaks in the Upland Forest CT and appears positively associated with height above MSWL; available phosphorus content; total woody detritus and tree covers; and representative age, and negatively with water duration. These relationships suggest that shrub biomass is severely affected by periodic flooding and its related effects.

Average shrub species richness per zone increases throughout the successional sequence, peaking in the Upland

Forest CT and seems positively associated with height above MSWL; available phosphorus content; total woody detritus, shrub, and tree covers; and representative age, and negatively with water duration and sodium content. These relationships indicate that increases in shrub diversity may reflect decreases in flooding effects and increases in shrub and tree covers.

Herb-Dwarf Shrub Stratum (Table 39)

This stratum is found in all CT's with the highest cover occurring in the polygenic Vascular Aquatic type. Total herb-dwarf shrub cover appears positively associated with organic matter content and total water cover, and negatively with sand, silt, and clay contents, and total detritus and mushroom covers. These relationships suggest that herb-dwarf shrub development is greater in low-lying sections of the Egg Lake study area having wet to moist Gleysolic soils.

Growth-form components of the bryoid and herb-dwarf shrub strata show variable biomass trends along the successional sequence. While bryoid, dwarf shrub, and shrub biomasses increase throughout the sequence, graminoid biomass decreases and forb biomass shows a bimodal pattern with peaks in the polygenic Vascular Aquatic and autogenic Upland Forest CT's.

Average herb-dwarf shrub species richness per zone shows a bimodal pattern with peaks in the polygenic

Wet Meadow and autogenic Upland Forest CT's and appears positively associated with available phosphorus content and total moss cover. These relationships indicate that increases in herb-dwarf shrub diversity are associated with decreased periodic flooding and its residual effects. The higher species diversity in the Wet Meadow CT compared to adjacent types probably reflects the transition between aquatic and terrestrial environments.

Total bare ground cover appears positively associated with organic matter; soil moisture; FC; and total liverwort cover, and negatively with sand, silt, and calcium carbonate contents, and S/C ratio. These relationships suggest that higher bare ground cover is found in low organic areas susceptible to hydrologic regime factors.

iii. Synthesis

Species presence and abundance patterns along the successional sequence are given in Table 39B. Species appear aligned primarily according to increasing height above MSWL and decreasing water duration and its associated effects. Drainage, physical and chemical soil properties, and vegetation cover also seem to contribute to variations in species abundances in the sequence. Topographic, physiographic, and hydrologic factors appear to restrict *Lemna trisulca*, *Acorus calamus*, *Ranunculus aquatilis* and nine other species in the herb-dwarf shrub

stratum to this study area.

Herbs such as *Potamogeton zosteriformis* and *Utricularia vulgaris* have their optima in the polygenic Vascular Aquatic CT. They generally tolerate most periodic hydrologic regime factors. These species help reduce flood-water velocity, promote sedimentation, and stabilize portions of this CT. The presence of an aquatic-terrestrial transition allows the dwarf shrub *Salix petiolaris* and herbs such as *Myriophyllum exalbescens*, *Bidens cernua*, and *Scolochloa festucacea* to attain their optima in the polygenic Wet Meadow CT. These species, tolerating most periodic flooding effects, promote additional sediment and organic build-up. With further improvements of the terrestrial environment, shrubs *Salix pseudomonticola* and *S. petiolaris*, the dwarf shrub *Picea glauca*, and herbs such as *Glyceria grandis* and *Eleocharis palustris* attain their optima in the polygenic Meadow CT. Except for *P. glauca*, these species generally tolerate most periodic flooding and drawdown periods and aid in accumulating litter and organic matter and in raising the substrate above MSWL. With a more ameliorated terrestrial environment, the tree *Salix bebbiana*, shrubs such as *S. pyrifolia*, *S. glauca*, and *S. bebbiana*, dwarf shrubs *S. bebbiana* and *Ribes hudsonianum*, and herbs such as *Carex atherodes*, *Galium trifidum*, *Calamagrostis canadensis*, *Urtica gracilis*, *Potentilla norvegica*, *Geum allepicum*,

and *Stellaria longifolia*, reach their optima in the polygenic Fen CT. These species and those from previous CT's apparently make minor changes in physical and chemical soil properties and help reduce wind velocity and incident radiation, permitting a more ameliorated terrestrial environment. With the absence of flooding and its related effects, trees such as *Populus balsamifera*, shrubs such as *Rosa acicularis* and *Viburnum edule*, dwarf shrubs such as *Viburnum edule*, and herbs such as *Poa palustris*, *Equisetum pratense* and *Rubus pubescens* attain their optima in the autogenic Upland Forest CT. Increasing height above MSWL and shelter from periodic flooding and its associated and residual effects are primary factors allowing succession to proceed.

To summarize, soil development, environmental stability, species diversity, and age generally increase throughout the successional gradient. Components of the understory biomass exhibit variable trends. Graminoids are the main contributors to total biomass in this study area. Total biomass in the Wet Meadow CT is the highest in the study region and is primarily a reflection of a relatively unstable aquatic-terrestrial transition. Of the biomass components, only bryoids, dwarf shrubs, and shrubs peak in the autogenic Upland Forest CT. Species diversity for each stratum peaks in the Upland Forest CT. Total species diversity in the Wet Meadow CT is generally

higher than in adjacent types as a probable result of the blending of aquatic and terrestrial environments.

Populus balsamifera/Rosa acicularis-Viburnum edule/V. edule is the most highly developed community in the EL study area. The average time required to achieve this community is *ca*. 110 years but varies from *ca*. 100 to 120 years via the shortest and longest seral pathways.

Periodic flood and fluctuating water regimes and subsequent drawdowns generally maintain Vascular Aquatic, Wet Meadow, Meadow, and Fen CT's in the TrS while the absence of flooding allows the Upland Forest CT to achieve the TeS. The influence of the hydrologic regime is sufficient to delay succession to the Upland Forest Type. However, complete absence of flooding and stabilization of water levels would allow succession to proceed uninterruptedly to the TeS.

E. Successional Sequences in the Nuphar Lake Study Area

i. Introduction

Four CT's, having 25 zones, are represented among the three sites in this study area (See Fig. 3, p.93 ; Pl. 5, p. 13). This area consists of a shallow back-water lake basin surrounded by Precambrian outcrops and high levees.

ii. Succession

Figure 8 shows the main successional sequences in the NL basin. Two distinct sequences are evident: the Peatland and the Upland. *Nuphar variegatum* is the initial colonizing herb of the EPS and is replaced by *Utricularia vulgaris* in the IPS. The latter species is followed by *Carex aquatilis* or *Lysimachia thyrsiflora* and, then, by the species complex (*Equisetum fluviatile-Eriophorum angustifolium-Menyanthes trifoliata*) in the LPS. These species are replaced by *Calla palustris* and *Potentilla palustris* in the LPS. Species in the IPS and LPS are found in the immature bog hummock section of the peatland sequence. *Potentilla* is replaced by *Lysimachia* in the ETrS. The latter is followed by *Oxycoccus microcarpus* in the ETrS and ITrS and, then, by *C. aquatilis* in the LTrS and TeS. The latter species is succeeded eventually by *Rubus chamaemorus* in the TeS. *Lysimachia* in the ITrS is followed by the species complex (*Smilacina trifolia-Epilobium palustre*) in the LTrS and, then, by *R. chamaemorus* in the TeS. These species occur in the mature bog hummock section of the sequence. *Lysimachia* is replaced by *Carex aquatilis* and *C. retrorsa* and/or *Calamagrostis inexpansa* in the ETrS and, then, by *C. canadensis* in the ITrS of the overmature bog hummock section in the upland sequence. The latter species is followed by *Fragaria vesca* and *Geocaulon lividum* in the LTrS. The latter species is succeeded by *Rubus acaulis* and, then,

Figure 8. Successional diagram for the Nuphar Lake study area, showing the sequence of community and soil types and the major species' replacements in the three vascular strata[a]. Refer to p. 238 for method of determining species replacements.

Legend:

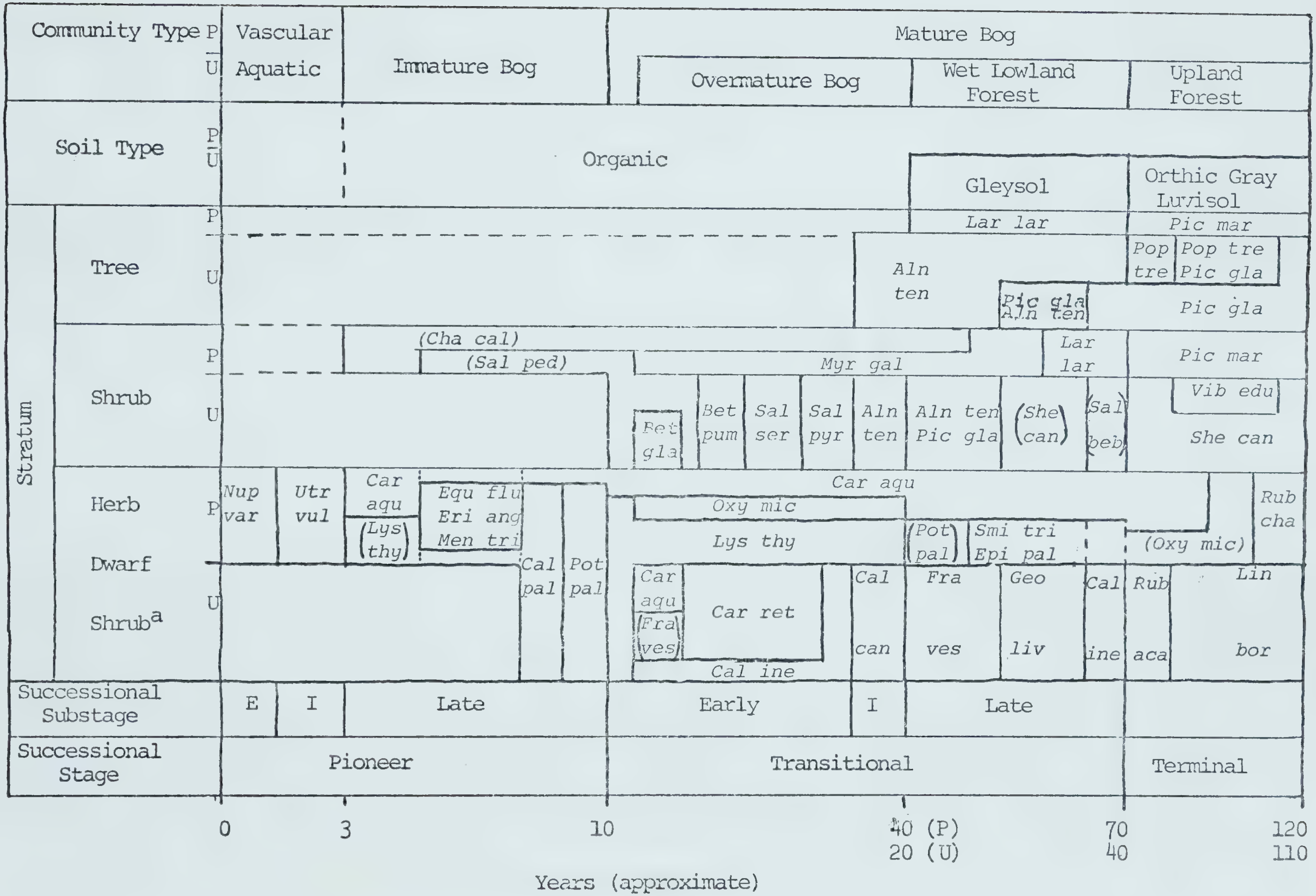
Aln ten:	*Alnus tenuifolia*	*Myr gal:*	*Myrica gale*
Bet gla:	*Betula glandulosa*	*Nup var:*	*Nuphar variegatum*
Bet pum:	*Betula pumila*	*Oxy mic:*	*Oxycoccus microcarpus*
Cal can:	*Calamagrostis canadensis*	*Pic gla:*	*Picea glauca*
Cal ine:	*Calamagrostis inexpansa*	*Pic mar:*	*Picea mariana*
Cal pal:	*Calla palustris*	*Pop tre:*	*Populus tremuloides*
Car aqu:	*Carex aquatilis*	*Pot pal:*	*Potentilla palustris*
Car ret:	*Carex retrorsa*	*Rub aca:*	*Rubus acaulis*
Cha cal:	*Chamaedaphne calyculata*	*Rub cha:*	*Rubus chamaemorus*
Epi pal:	*Epilobium palustre*	*Sal beb:*	*Salix bebbiana*
Equ flu:	*Equisetum fluviatile*	*Sal ped:*	*Salix pedicellaris*
Eri ang:	*Eriophorum angustifolium*	*Sal pyr:*	*Salix pyrifolia*
Fra ves:	*Fragaria vesca*	*Sal ser:*	*Salix serissima*
Geo liv:	*Geocaulon lividum*	*She can:*	*Shepherdia canadensis*
Lar lar:	*Larix laricina*	*Smi tri:*	*Smilacina trifolia*
Lin bor:	*Linnaea borealis*	*Utr vul:*	*Utricularia vulgaris*
Lys thy:	*Lysimachia thyrsiflora*	*Vib edu:*	*Viburnum edule*
Men tri:	*Menyanthes trifoliata*		

[a] Dwarf shrubs have been omitted from the herb-dwarf shrub stratum.

P: Peatland sequence. E: Early

U: Upland sequence. I: Intermediate

(): Species sometimes absent.


Community Type
P
U
Vascular Aquatic
Immature Bog
Mature Bog
Overmature Bog
Wet Lowland Forest
Upland Forest
Soil Type
Organic
Gleysol
Orthic Gray Luvisol
Stratum
Tree
Lar lar
Pic mar
Aln ten
Pop tre
Pop tre Pic gla
Pic gla Aln ten
Pic gla
Shrub
(Cha cal)
(Sal ped)
Myr gal
Lar lar
Pic mar
Bet gla
Bet pum
Sal ser
Sal pyr
Aln ten
Aln ten Pic gla
(She can)
(Sal beb)
Vib edu
She can
Herb
Dwarf Shrub[a]
Nup var
Utr vul
Car aqu
(Lys thy)
Equ flu Eri ang Men tri
Cal pal
Pot pal
Car aqu
Oxy mic
Lys thy
(Pot pal)
Smi tri Epi pal
(Oxy mic)
Rub cha
Car aqu
(Fra ves)
Car ret
Cal ine
Cal can
Fra ves
Geo liv
Cal ine
Rub aca
Lin bor
Successional Substage
E
I
Late
Early
I
Late
Successional Stage
Pioneer
Transitional
Terminal
0
3
10
40 (P)
20 (U)
70
40
120
110
Years (approximate)

Linnaea borealis in the TeS.

In the peatland sequence, *Chamaedaphne calyculata* is the initial colonizing shrub of the IPS, followed either by *Salix pedicellaris* in the LPS and ETrS and, then, *Myrica gale* in the ETrS and ITrS or by *M. gale* in the LTrS. *Myrica* is followed by *Larix laricina* in the LTrS. The latter species is succeeded by *Picea mariana* in the TeS. In the upland sequence, *S. pedicellaris* in the ETrS is replaced, in turn, by *Betula glandulosa*, *B. pumila*, *Salix serissima*, and *S. pyrifolia*. These species dominate in the over-mature bog section. *Salix pyrifolia* is replaced by *Alnus tenuifolia* in the ITrS and LTrS. This species is followed by *Picea glauca* in the LTrS. *Picea* is succeeded eventually by *Viburnum edule* and, then, *Shepherdia canadensis* in the TeS.

In the peatland sequence, *Larix laricina* is the initial colonizing tree in the LTrS and is succeeded by *Picea mariana* in the TeS. In the upland sequence, *Alnus tenuifolia* in the ITrS and LTrS is replaced either by the species complex (*Picea glauca-Alnus tenuifolia*) in the LTrS or by *Populus tremuloides* in the TeS. The species complex is succeeded by *P. glauca* in the LTrS and TeS while *P. tremuloides* is succeeded by the species complex (*P. tremuloides-P. glauca*) and, then, *P. glauca*, the terminal species of this sequence.

For the herb-dwarf shrub stratum, Raup (1935:35) recognized only *Nuphar variegatum*, *Menyanthes trifoliata*,

Carex aquatilis, *C. retrorsa*, and *Calamagrostis inexpansa* as in Figure 8. Dirschl *et al.* (1974:30) recognized only *Nuphar*, *Potentilla*, and *Menyanthes* as in Figure 8. However, Dirschl also included *Potamogeton*, *Myriophyllum*, *Ranunculus*, *Scirpus*, *Typha*, *Phragmites*, *Carex*, and *Acorus* in his successional sequence for meander scrolls and backswamps. Except for *Scirpus* spp., *Phragmites communis*, *Carex rostrata*, and *Acorus calamus*; the above genera, as well as *Petasites sagittatus* mentioned by Raup, were also found in the study area but did not attain sufficient prominence to be named as part of a community by the author.

For the shrub stratum, Raup recognized *Chamaedaphne calyculata*, *Betula glandulosa*, and *Salix pyrifolia* while Dirschl recognized only *S. pedicellaris* as in Figure 8. However, Dirschl also included *Ledum groenlandicum* and *Andromeda polifolia* in his sequence. These species as well as *Salix myrtillifolia* mentioned by Raup, were also found in this study area but did not attain sufficient prominence to be named as part of a community by the author. *Kalmia polifolia* mentioned by Dirschl in his sequence does not occur in this or other study areas.

For the tree stratum, Raup only recognized *Picea mariana* while Dirschl noted *Larix laricina* and *P. mariana* as in Figure 8. Both Raup and Dirschl acknowledge the development of hypnic spp. to sphagnum spp., then to *P. mariana*. However, neither investigator mentioned stages in hummock development and relationships of Bog

and Upland CT's. The lack of similarity between this and former studies may be the result of the general nature of their studies which were limited only to certain parts of the bog.

Population analysis of major tree species (Table 40) along the successional sequence indicate that environmental conditions in the Vascular Aquatic CT exclude all species. However, conditions in the Bog CT allow *Alnus tenuifolia* and *Salix bebbiana* to grow but still are not suitable as both species die off after the transgressive class. *Picea glauca* and *Salix arbusculoides* die off after the sapling class is reached. *Larix laricina* and *P. mariana* show their best growth in this CT, except die-off generally occurs after sapling development is achieved. In the Wet Lowland Forest CT, *S. bebbiana*, *Populus balsamifera*, *Alnus tenuifolia*, and *Salix arbusculoides* have their highest densities. Only *P. glauca* shows any growth in higher tree classes. In the Upland Forest CT, biotic interactions may be present but are not particularly evident as *P. glauca* followed by *P. tremuloides* attain their best growth.

Tree Stratum (Table 41)

This stratum is found in autogenic Bog, Wet Lowland Forest, and Upland Forest CT's. The sheltered location at the bottom of granitic outcrops, in conjunction with run-off, may be important to the highest tree

Table 40. Mean densities per hectare of stem size classes of major tree species in three community types along the upper segment of the successional gradient in the Nuphar Lake study area.

Tree	SC[a]	Community Type[b,c]		
		16	15	13
		16	*3*	*3*
Larix laricina	sdl[d]	1750	.	.
	trs	1530	.	.
	sap	35	.	.
Picea glauca	sdl	380	4000	3330
	trs	.	3670	1830
	sap	5	773	1650
	1	.	160	293
	2	.	27	27
	3	.	27	53
	4	.	.	53
Picea mariana	sdl	1380	.	.
	trs	810	.	.
	sap	60	.	.
Populus balsamifera	sdl	.	.	.
	trs	.	170	.
	sap	.	80	.
Populus tremuloides	sdl	.	.	.
	trs	.	.	1000
	sap	.	27	2110
	1	.	.	1230
Salix arbusculoides	sdl	.	.	.
	trs	.	2500	27
	sap	190	587	27
	1	.	27	.
Salix bebbiana	sdl	.	2000	667
	trs	160	12200	167
Alnus tenuifolia	sdl	1250	6670	.
	trs	1500	6330	500
	sap	.	720	27
	1	.	27	27

[a] Size Class.
[b] Community Type: 16) Bog, 15) Wet Lowland Forest, 13) Upland Forest.
[c] Number of zones in the study area given in italicized numbers.
[d] sdl = seedlings; trs = transgressives; sap = saplings; and tree dbh classes: 1 = 8-13, 2 = 13-18, 3 = 18-23, 4 = 23-28 cm.

gradient in the Hughes Lake study area.

along the successional gradient in the Hughes Lake study area.

A. Soil Physical Properties
Soil Temperature (°C)
Sand/Clay Ratio
Sand %
Silt %
[illegible]
Available Water %
[illegible]
Available Nitrogen (kg/ha)
Ammonium Carbonate
[illegible]
Sulphate
[illegible]
Herb-layer
Shrub %
Bare Ground %
[illegible]
Yield (kg/ha)
[illegible]

Species Composition

Picea mariana		[illegible]		
Alnus tenuifolia		[illegible]		
Salix arbusculoides		[illegible]		
Populus balsamifera		[illegible]		
Betula papyrifera		[illegible]		
Populus tremuloides		[illegible]		
[illegible]				
Picea mariana				
[illegible]				
S. barklayi (?)		[illegible]		
[illegible]				
Carex limosa				
Andromeda polifolia				
[illegible]				
Typha latifolia				
Bidens cernua				
Cicuta douglasii				
Rubus chamaemorus				
Mentha arvensis				
Rumex occidentalis				
[illegible]				
Smilacina trifolia				
[illegible]				
Ranunculus gmelinii			7	
Sium suave				
Galium trifidum				
[illegible]				
Salix myrtillifolia				
[illegible]				
Salix barklayi (?)				
Calamagrostis inexpansa				
[illegible]				
Equisetum scirpoides				
[illegible]				
Fragaria vesca				
Picea glauca				
[illegible]				
Linnaea borealis				
[illegible]				
Maianthemum canadense				
Poa pratensis				
[illegible]				
Ribes hudsonianum				
[illegible]				
Cornus stolonifera				
[illegible]				
Poa palustris				
Equisetum pratense				
[illegible]				
Mertensia paniculata				
[illegible]				
Rosa acicularis				
Viburnum edule				
Shepherdia canadensis				
Cornus canadensis				
Ribes oxyacanthoides				
Rubus acaulis				30
[illegible]				8
Mitella nuda				3
Rubus strigosus				7
[illegible]				3
[illegible]				8
Galium boreale				
[illegible]				
[illegible]				
[illegible]				

Community Types: 2) Vasc[illegible] [illegible] forest, [illegible] Upland forest.
[illegible] of zones given in italicized numbers.
[illegible] 15 cm level on 29 September 1971.
[illegible] data available.
Conversion scale: insignificant (0.5), L⁻(2), [illegible], L⁺(4), M⁻(5), M(6), M⁺(7), H⁻(8), H(9), H⁺(10).
Mean of % cover-class mid-points.
[illegible]
[illegible] in one community type and having a [illegible] are not listed, see species/zone tables [illegible] compositions of zones.
* [illegible] this study area (herb dwarf shrubs, *Sparganium eurycarpum*, *Carex brunnescens*, *C. lasiocarpa*, [illegible], *Eriophorum brachyantherum*, *Salix serissima*, *Vaccinium vitis-idaea*, *Petasites frigidus* [illegible] in the table).

cover occurring in the Wet Lowland Forest CT.

Average tree species richness per zone is highest in the Wet Lowland Forest CT. The higher species diversity in this type compared to adjacent types probably reflects the transition between two environmental extremes.

Shrub Stratum (Table 41)

Total shrub cover is fairly constant among the Bog, Wet Lowland Forest, and Upland Forest CT's.

Shrub biomass apparently increases throughout succession, peaking in the Upland Forest CT.

Average shrub species richness per zone, peaking in the Bog CT, generally decreases throughout the sequence. Shrub diversity seems positively associated with total shrub cover and representative age, and negatively with total water and bare ground covers. These relationships indicate that increases in shrub diversity may reflect decreasing influence of surface water.

Herb-Dwarf Shrub Stratum (Table 41)

This stratum is found in all CT's, with the highest cover occurring in the Vascular Aquatic CT.

Growth-form components of the byroid and herb-dwarf shrub strata show different biomass trends along the successional sequence. While dwarf shrub and shrub biomasses increase throughout the sequence, forb biomass decreases. Byroid and graminoid biomasses peak in the Bog CT.

Average herb-dwarf shrub species richness per zone peaks in the Wet Lowland Forest CT. Comparatively higher values for herb-dwarf shrub diversity in Bog and Wet Lowland Forest CT's are the result of microtopographic variations in the former type and of a transition between two environmental extremes in the latter type.

iii. Synthesis

Species presence and abundance patterns along the successional sequence are given in Table 41B. Species appear aligned according to increasing height above MSWL and decreasing influence of the hydrologic regime in the NL basin. Soil drainage and physical and chemical soil properties also seem to contribute to differences in species abundances in the sequence. Topographic, physiographic, and hydrologic factors appear to restrict *Larix laricina* and *Picea mariana* in the tree stratum, *Myrica gale*, *Salix pedicellaris* and 9 other species in the shrub stratum, and *Nuphar variegatum*, *Sparganium minimum*, and 42 other species in the herb-dwarf shrub stratum to this study area.

Herbs such as *Nuphar variegatum* and *Utricularia vulgaris* have their optima in the Vascular Aquatic CT. These species can tolerate deep, sediment-free waters whose levels are stable and thus help promote organic build-up of the lake basin. The presence of a terrestrial environment permits trees *Larix laricina* and *Picea*

mariana, shrubs such as *Myrica gale* and *Salix serissima*, dwarf shrubs such as *Myrica gale* and *Salix pyrifolia*, and herbs such as *Potentilla palustris* and *Carex aquatilis* to attain their optima in the Bog CT. They can tolerate only non-flooded organic soils having very low temperatures, very high moisture, and ice conditions. These species, in extending the areal extent of the floating mat, produce litter and organic build-up which eventually raises the substrate above MSWL. Further improvements of the terrestrial environment allow trees such as *Alnus tenuifolia*, *Populus balsamifera*, and *Betula papyrifera*, shrubs such as *Salix myrtillifolia*, *A. tenuifolia*, and *S. arbusculoides*, dwarf shrubs such as *Salix barklayi (?)*, *Picea glauca*, *Betula papyrifera*, and *Cornus stolonifera*, and herbs such as *Calamagrostis canadensis*, *Fragaria vesca*, *Poa pratensis*, *Geocaulon lividum* to attain their optima in the Wet Lowland Forest CT. These species and those from previous CT's apparently make minor changes in soil properties and reduce wind velocity and incident radiation, permitting a more ameliorated environment. Further increases in height and drainage permit trees *Picea glauca* and *Populus tremuloides*, shrubs such as *Shepherdia canadensis* and *Viburnum edule*, and dwarf shrubs *Arctostaphylos uva-ursi*, *Rosa acicularis*, and *Salix pseudo-monticola*, and herbs such as *Linnaea borealis*, *Cornus canadensis*, and *Galium boreale* to reach their optima in

the Upland Forest CT. Increasing height above MSWL and decreasing influence from the lake-water regime are primary factors allowing succession to proceed.

To summarize, soil development, environment stability, and age generally increase throughout the successional gradient. Components of the understory biomass exhibit variable trends. While dwarf shrub and shrub biomasses increase, bryoid, graminoid, and forb biomasses decrease along the sequence. Shrub species richness peaks in the Bog CT, while herb-dwarf shrub and tree species richnesses peak in the Wet Lowland Forest CT. Total species diversity in the Wet Lowland Forest CT is higher than in adjacent types as this type forms a transition between two environmental extremes.

Picea mariana/P. mariana/Myrica gale is the most highly developed community in the bog section of the successional sequence in the NL study area. The average time required to achieve this community is *ca.* 120 years but varies from *ca.* 110 to 130 years using the shortest and longest seral pathways. *Picea glauca/Shepherdia canadensis/Rosa acicularis* is the most highly developed community in the upland section. The average time entailed to reach this community is *ca.* 110 years but varies from *ca.* 100 to 120 years via the shortest and longest pathways.

Plant succession in the NL study area is controlled

by autogenic factors. Absence of over-levee flooding and stabilization of lake water-levels not only contributes to the development and maintenance of bog communities but also allows succession to proceed to the LTeS.

F. Synthesis for the Study Region

Figure 9 summarizes the successional relations of the 16 plant community types recognized in the northeastern portion of the PA delta; it may also be regarded as a two-dimensional direct ordination of CT's along complex gradients of soil moisture and flood frequency. Closely associated with flood frequency are successional factors (Allogenic, Polygenic, and Autogenic) which generally correspond to successional stages (Pioneer, Transitional, and Terminal); to geomorphological deltaic processes (Active, Semi-Active, and Inactive); and to surface drainage status (Open, Restricted, and Isolated).

A simplified CT successional sequence for the RC study area taken from Figure 9 is:

```
       (CT #1)                  (9)              (10)
Water (Algal Aquatic) ---> Levee Herb ---> (Swale Shrub)
          \                     ↑           ↗    ↓
           ↘                    |         /      
             Herb Immature Marsh       Levee Shrub (11)
                  (3)                      ↓
                                       Levee Tree (12)
                                           ↓
                                      Upland Forest
                                          (13)
```

Figure 9. Successional relations of plant community types (CT's) in those parts of the study region, leading to the *Picea glauca/Rosa acicularis/Viburnum edule* climax Community Type. Estimated number of years required for replacement is given in italicized numbers.

Legend:

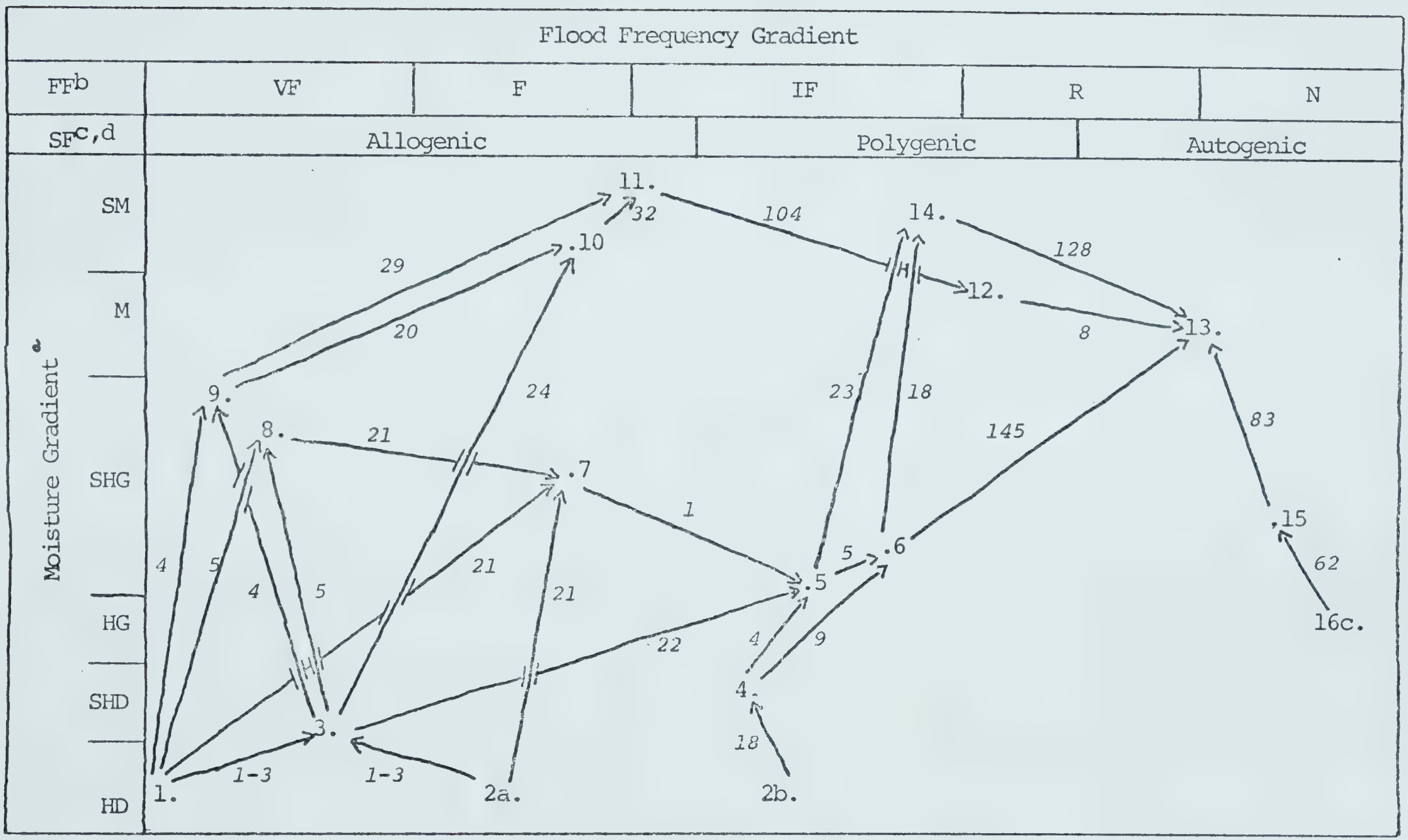
1. Algal Aquatic CT in the Revillon Coupé and Lake Athabasca Marsh study areas
2. *Utricularia vulgaris* (Vascular Aquatic) CT
   a. *Glyceria striata* ST in the Chilaway Snye study area
   b. *Lemna trisulca* ST in the Egg Lake study area
3. *Equisetum fluviatile* (Herb Immature Marsh) CT
4. *Carex atherodes* (Wet Meadow) CT
5. *Salix petiolaris/Carex atherodes* (Meadow) CT
6. *Salix bebbiana/S. bebbiana/Carex atherodes* (Fen) CT
7. *Salix lutea/Carex atherodes* (Marsh) CT
8. *Salix interior/Typha latifolia* (Shrub Immature Marsh) CT
9. *Salix interior/Equisetum arvense* (Levee Herb) CT
10. *Alnus tenuifolia/Epilobium angustifolium* (Swale Shrub) CT
11. *Alnus tenuifolia/Cornus stolonifera* (Levee Shrub) CT
12. *Populus balsamifera/Cornus stolonifera/Equisetum pratense* (Levee Tree) CT
13. *Picea glauca/Rosa acicularis/Viburnum edule* (Upland Forest) CT
14. *Salix bebbiana/S. bebbiana/Equisetum pratense* (Moist Lowland Forest) CT
15. *Picea glauca/Alnus tenuifolia/Geocaulon lividum* (Wet Lowland Forest) CT
16. *Myrica gale/M. gale* (Bog) CT
    c. *Alnus tenuifolia/Fragaria vesca* (Overmature Hummock) ST

a. HD: Hydric, SHD: Subhydric, HG: Hygric, SHG: Subhygric, M: Mesic SM: Submesic. The CT's were assigned to different moisture classes according to criteria presented on p. 21.

b. FF: Flood Frequency - VF: Very Frequent, F: Frequent, IF: Infrequent, R: Rare, N: Never.

c. SF: Successional Factor.

d. Remaining associated factors on p. 306.



Flood Frequency Gradient
FFb
VF
F
IF
R
N
SFc,d
Allogenic
Polygenic
Autogenic
Moisture Gradienta
SM
M
SHG
HG
SHD
HD
1.
2a.
2b.
3.
4.
.5
.6
.7
8.
9.
.10
11.
12.
13.
14.
.15
16c.
1-3
1-3
4
5
4
5
21
29
20
24
21
21
22
1
32
104
128
8
23
18
145
5
4
9
18
83
62

These CT's are comparable to Shore, Shrub, and Tree Associations in the successional sequence for local river deposits described by Raup (1935:88). Except for Swale Shrub, these CT's are also comparable to Shore, Shrub, and Forest Communities occurring in the successional sequence for flowing channels described by Dirschl *et al*. (1974:30). Based on age data for communities, the average time required to reach the Upland Forest CT is *ca*. 140 years.

A simplified CT successional sequence for the LAM study area taken from Figure 9 is:

```
       (CT #1)                     (3)
Water (Algal Aquatic) ——> (Herb Immature Marsh)
                                    ↓
                          Shrub Immature Marsh (8)
                                    ↓
                                 Marsh (7)
```

Herb Immature Marsh, Shrub Immature Marsh, and Marsh CT's are comparable to the Shore, Shrub, and Tree Associations in the successional sequence for the delta plains described by Raup (1935:88) and to the Shore, Shrub, and Forest Communities of Dirschl *et al*. (1974:30). Both investigators recognized an aquatic type dominated by *Potamogeton* and a meadow type. The former type is recognized in this study as an Algal Aquatic CT lacking vascular macrophytes. The latter type is incorporated into the Marsh CT. Based on age data for communities, the average time required to reach the Marsh CT is *ca*. 35 years. The Marsh CT is not replaced by the Meadow Type due to allogenic factors.

A simplified CT successional sequence for the CS study area taken from Figure 9 is:

```
    (CT #2a)                (7)        (5)              (6)
Vascular Aquatic ──> Marsh ──> Meadow    ──>       (Fen)
                                                        ↓
   ╲                                    ↗      (14)Moist Lowland Forest
    ↘  Herb Immature Marsh                              ↓
              (3)                          (13) Upland Forest
```

These CT's are comparable to the Aquatic, Shore, and Tree Associations in the successional sequence for partially ponded creeks described by Raup (1935:88); and Aquatic, Shore, and Forest Communities of Dirschl *et al.* (1974:30). Meadow and shrub types recognized by both investigators are incorporated into Meadow and Fen CT's here. Based on age data for communities, the average time to reach the Upland Forest CT is *ca.* 170 years.

A simplified CT successional sequence for the EL study area taken from Figure 9 is:

```
    (CT #2b)                  (4)            (5)         (6)
Vascular Aquatic ──>  Wet Meadow ──> (Meadow) ──> Fen
                                                       ↓
                                               Upland Forest
                                                    (13)
```

These CT's are comparable to Aquatic and Tree Associations of Raup (1935:88); and Aquatic and Forest Communities of Dirschl *et al.* (1974:30). Shore, meadow, and shrub types recognized by both investigators are incorporated into Wet Meadow, Meadow, and Fen CT's. Based on age data for communities, the average time required to reach the Upland

Forest CT is *ca.* 110 years.

A simplified CT successional sequence for the NL study area taken from Figure 8 with the upland sequence also shown in Figure 9 is:

Peatland Climax
↑
Vascular Aquatic ⟶ Bog (immature ⟶ mature hummocks)
↓
(CT #16c) overmature hummocks
↓
(15) Wet Lowland Forest
↓
(13) Upland Forest

These CT's are comparable to the Aquatic and Tree Associations of Raup (1935:29,35); and Aquatic and Forest Communities of Dirschl *et al.* (1974:30). Shore, meadow, and shrub types recognized by both investigators are incorporated into the Bog CT. Based on age data for communities, the average time required to reach the peatland climax stage in the bog sequence is *ca.* 120 years; the upland climax is achieved in *ca.* 110 years.

Picea glauca/Rosa acicularis/Viburnum edule is the most highly developed, stable, and common upland climax CT in the study region. The average time required to achieve this CT is *ca.* 170 years, but varies from 140 to 180 years using the shortest and longest pathways. The *Picea mariana/P. mariana/Myrica gale* community is a peatland climax reached via the bog sequence described from the NL study area.

Topography, hydrology, soil texture, soil moisture, soil drainage, soil temperature, and soil nutrient regime are recognized as important factors influencing species and vegetation distribution patterns and successional relationships in the study region. The relative importance of each factor, however, varies among the five study areas and their successional sequences.

Environmental stability increases in each sequence, resulting from a decreasing trend in annual and periodic floodings and their associated and residual effects, and from an increasing trend in topographic and physiographic controls.

Modification of the microclimate usually increases along successional sequences in the study region. Amelioration of extremes of air temperature and relative humidity, and decreases in wind speed and light intensity at ground level occurred with progressive development of shrub and tree strata.

Vascular plant species diversity generally increases along each sequence. Low species diversities occur in Levee Herb, Levee Shrub, and Levee Tree CT's because of localized stress from annual and periodic flooding effects, and in the Moist Lowland Forest CT because of periodic flooding. High species diversities are found in Meadow and Bog CT's as a result of large

micro-topographic variations (hummock-hollow complexes) and in Wet Meadow and Wet Lowland Forest CT's because of the formation of a transition between two environmental extremes. Species diversity generally does not reflect community stability but environmental stability. Thus, a decrease in diversity is to be expected in certain successional stages where disturbance is so frequent and devastating that species adapted to stability have never become well established.

Understory growth-form components change in relative biomass with succession. Shrubs tend to dominate in the pioneer stages; graminoids and dwarf shrubs in the transitional stages; forbs in transitional and terminal stages; and bryoids in terminal stages. Edaphic factors appear more important than species diversity in contributing to biomass accumulation.

The sequence of dominant vascular growth-forms during the terrestrial section of hydrarch succession in the five study areas is very consistent, *i.e.* from graminoids to broad-leaf deciduous shrubs to broad-leaf deciduous trees to needle-leaf trees. Within the herb-dwarf shrub stratum there is a distinct shift from dominance by graminoids in early stages to dominance by forbs and dwarf shrubs in late stages. Where one growth-form maintains an important quantitative role for extended periods, there is frequently a significant

turnover in dominant species, *e.g.* of *Salix* in the shrub stratum. Thus plant succession shows definite and recurring physiognomic as well as floristic trends from aquatic to upland habitats in the study region.

Structural complexity, biotic interaction, and the ages of the oldest plants increase with succession. Communities of the same CT are similar in physiognomy and species composition but may vary widely in age. These age differences frequently result from local hydrologic variations among and within study areas, or from variations in the rate of accumulation of organic matter (*e.g.*, in the NL study area). Communities and CT's which are species-poor have simple structures and are more influenced by flooding and local edaphic factors, while species-rich and complex-structured ones are more affected by macroclimatic and biotic factors.

Dirschl (1973:J17) estimated 110 years to be the time necessary to achieve a mature Coniferous Forest Type during a long-term decline in water levels in the southern portion of the PA delta. Based on age data for CT's in the study region (Fig. 9), it is believed that an Upland Forest CT comparable to Dirschl's type is attained in *ca.* 170 years. The 60-year difference in the time required to complete this major chronosequence between the two study regions may be traceable to significant differences in sedimentation, site stability and age, the absence of one or more seral stages and, hence, succession

rates; and/or in the methods employed, and, hence, the results obtained. The species composition and seral sequences reported by Raup (1935) and Dirschl *et al.* (1974) have much in common, but do not include many of the species and successional CT's reported here. Of the five study areas investigated, the Egg Lake area has most in common with the botanical patterns and trends described in Raup and Dirschl, followed in decreasing order by the CS, LAM, RC, and NL study areas. This thesis has attempted to describe the wide spectrum of botanical variation found inthe study region, without assessing the relative extents of different CT's or relative frequencies of seral sequences. Such work remains to be done over much of the PA delta before a true appreciation of its complexity and dynamics can be gained.

The term "climax" as used in this thesis refers to species and vegetation units which are in dynamic equilibrium with existing climatic, geomorphological, edaphic, and biotic conditions. It describes the relative stability of a mature community which is able to remain substantially unchanged for a long period compared to other communities in the study region. Climax communities are composed of populations with stable age- and size-distributions. Three climax tree species are recognized in the study region by the author: *Picea glauca*; *P. mariana*, and *Pinus banksiana*. *Picea glauca* is

dominant in the Upland Forest CT; it is considered to be the "climatic climax" species in northern Alberta by White (1915), Moss (1932, 1953a), Raup (1935, 1946), and Rowe (1953). Because of its different developmental history in floodplain levees and terraces of the PA delta, the climax *P. glauca/Rosa acicularis/Viburnum edule* should probably not be grouped together with other climax vegetation units dominated by *P. glauca* in non-alluvial areas of northern Alberta. Dirschl *et al.* (1974:21,30) recognized *P. glauca* as the dominant species with *Abies balsamea* as a common associate in the Athabasca River section of the delta. The latter species has not been found in the study region; elsewhere on the delta, local site conditions seem to determine whether *P. glauca* or *A. balsamea* becomes dominant (Rowe 1961).

Picea mariana is dominant in the Bog CT and *Pinus banksiana* in the Precambrian Outcrop CT's, and both are regarded as "edaphic climax" species. The former is found on poorly drained peatlands of isolated basins not influenced by over-levee flooding. Moss (1953a) interpreted *P. mariana* as an edaphic climax species well adapted to both poor drainage and periodic burning. *Pinus banksiana* occurs on rapidly drained lithic soils of high outcrops unaffected by flooding. Moss (1955) suggested that components of his *P. banksiana* consociation may form an edaphic climax on poor, dry sites, whereas others

follow periodic burning on better sites. Pyric disturbance does seem to be a major influence on rock outcrops, along with strong topographic controls, weak soil development, and excessive drainage. Available evidence from the NL study area suggests that *P. glauca* could eventually succeed *P. mariana* if organic build-up or decline in water-table levels are highly accentuated, and also *P. banksiana* if soil moisture relations improve and soil development is greatly promoted.

Succession is much more rapid in the relatively fertile lowlands of the other four areas. Where the topographic gradient is steep, as in the RC study area, seral stages are highly compressed and sharply delineated. Where the gradient is gentle, seral stages are very extensive and grade into each other more gradually. Beals (1969) also found that the discreteness of vegetation zonation increases with the steepness of the environmental gradient. Forbs appear to tolerate flooding only where there is rapid drainage while most graminoids evidently can not tolerate flowing water regimes on rapidly drained soils. Subsequent to flooding the rate of drainage and accompanying physical and chemical changes in waters and soils determines the type of flora. For example, rapid soil drainage appears to result in invasion of herbs and grasses on fresh sediment, while slow drainage favours the persistence of sedges on

predominantly organic substrates.

An inner floating *Carex* mat occurs between mature bog communities and open water around the entire NL basin. The outer margins of the Bog CT appear to have been waterlogged as evidenced by the die-off of several upland species (*e.g.*, *Betula papyrifera*). As these more hydric conditions persisted *Sphagnum*-dominated communities with hummocky microtopography became established. With the presence of *Sphagnum* mosses, ombrotrophic conditions are favoured as available nutrients are fixed in undecomposed plant matter. The mat surface contains many young bog species which are small-sized but increasing in cover. Still, species diversity is fairly high due to the microhabitats found in the pronounced hummock-hollow complexes. This study was not concerned with different alternating stages of the hummock-hollow regeneration cycle recorded by M. S. Moss (1949) and E. H. Moss (1953a). However, a progression from immature to mature to overmature hummock stages was revealed in the herb-dwarf shrub stratum. Even though many of the overmature hummocks probably degenerate to the immature hollow stage the overall trend is for the former stage to increase in relative area such that succession toward the Wet Lowland Forest CT is quite evident.

In much of the study region, annual flooding has clearly prevented many communities of the Marsh CT and

other lowland types from undergoing succession to the Upland Forest CT. In the PA delta as a whole, flooding and not burning is the dominant factor retarding hydrarch succession. As long as water levels remain stable, the successional process proceeds uninterruptedly toward the climatic climax for the study region.

CONCLUSIONS

The vascular flora of the study region is characterized by 59 families, 160 genera, and 292 species. Largest families in order of decreasing species numbers are Gramineae, Cyperaceae, and Compositae. This study has increased our knowledge of the floristic composition of the Peace-Athabasca delta by the addition of 21 new vascular species. The species diversity of the delta communities is higher than, and contrasts sharply with, those of non-deltaic regions in northeastern Alberta.

Using the cluster analysis method of Pritchard and Anderson (1971) with species cover data, the 165 sampled zones were classified by the author into 16 community types and six subtypes. The physiognomic and floristic criteria employed in this process have proved to be quite suitable for elucidation of important ecological patterns and successional relationships of plant species and communities in the Peace-Athabasca delta region. The community types have much in common with those previously described in a more subjective manner by other investigators in this and other deltaic regions of the boreal zone in Canada.

The positions of the community types in Figure 9 represent their optima, *i.e.* where their fullest expression occurs. Thus each community type occupies a relatively distinct position in the deltaic landscape. Vegetational discontinuities on the ground result from abrupt changes in flood-water duration, edaphic variables, and geomorphological history. Vegetational continuity is prevalent where these changes are more gradual.

Communities in the study region are controlled by either allogenic, polygenic, or autogenic factors. The relative control exerted by these factors determines the physiognomy, composition, and stability of the communities. Communities of one community type may retrogress to those of earlier stages depending on the degree of disturbance caused by annual and periodic floodings, or they may proceed to community types of later seral stages in the absence of floodings.

Plant succession is driven mainly by allogenic factors in the Revillon Coupé, Lake Athabasca Marsh, and Chilaway Snye study areas; by polygenic factors in the Egg Lake study area; and by autogenic factors in the Nuphar Lake study area. Hydrologic, topographic, and edaphic factors influence plant establishment, distribution, and succession. Variations in the rates of erosion and sedimentation, the frequency and magnitude of water-level fluctuations, and the duration of floods are

the major hydrologic determinants of both horizontal and vertical distribution patterns of species, communities, and community types in four of the five study areas. Edaphic factors including texture, moisture, drainage, temperature, and nutrients are important secondary controls.

The following environmental trends are associated with hydrarch succession in the study region:

1. Flood-water duration, flood frequency, sand content, sand/clay ratio, available potassium, soil temperature extremes, and bare ground cover generally decrease with succession, and attain their highest values in allogenic areas. These factors are regarded as major effects of annual flooding.

2. Silt content, soil pH, and calcium carbonate initially increase then decrease with succession, and generally peak in polygenic areas. These factors are also associated with annual and periodic floodings.

3. Height above mean summer water level, substrate stability, clay content, organic matter, and available phosphorus generally increase with succession and attain their highest values in autogenic areas which are rarely, if ever, flooded.

4. Moisture and drainage conditions for upland plants improve and dependence on local precipitation as a water source increases, with succession.

5. Allogenic areas are generally characterized by orthic regosols, rego gleysols, and gleyed regosols. In upper sections of polygenic areas cumulic regosols are usually prominent, while in lower sections orthic gleysols predominate. In upper sections of autogenic areas orthic gray luvisols are normally dominant, while in lower sections organic soils prevail. Stages of plant succession correspond closely to those of soil development in the study region.

6. Air temperature and relative humidity range, and wind speed and light intensity decrease at ground level with the progressive development of shrub and tree strata. Thus, modification and amelioration of community microclimate, and total environmental stability usually increase along the successional gradient in the study region.

The following community trends are associated with hydrarch succession in the study region.

1. Physiognomic complexity, age, and biotic interaction generally increase with succession.

2. Forb, dwarf shrub, and total understory biomass and species richness generally increase with succession.

3. Graminoid biomass generally decreases with succession.

4. Shrub biomass peaks in the middle stages of succession while shrub species richness increases with succession.

Species diversity seems to be a function of both community stability and environmental stability. Understory biomass is controlled by overstory development and edaphic variables and is not well associated with understory species diversity. Species in the herb-dwarf shrub stratum are better indicators of succession than those in either the shrub or tree stratum.

Water-level fluctuations in the Peace-Athabasca delta may be grouped into four categories:

1. Spring flooding, which is the most pronounced in the study region, is effected by lowland watershed runoff and involves ice-jams.

2. Summer flooding from mountain watersheds occurs, especially, after periods of exceptionally warm weather. During spring and summer floods log-jams, beaver and hydrologic dams, and levees modify basic flooding patterns.

3. Summer flooding induced by easterly wind-tides from Lake Athabasca causes irregular and sudden fluctuations of water levels in those study areas connected by distributaries to the lake.

4. Rhythmic diurnal fluctuations throughout the growing season are of smaller magnitude than the first three, and affect only communities on slip-off slopes and cut-banks adjacent to channels. The flora and vegetation of the study region are well adjusted to these natural fluctuations in the hydrologic regime. Annual flooding

has clearly inhibited levee herb, levee shrub, herb immature marsh, shrub immature marsh, and marsh; and periodic flooding has retarded levee tree, wet meadow, meadow, and fen from undergoing further succession to the upland forest communities. In the Peace-Athabasca delta, unlike most other parts of boreal Alberta, flooding and not burning is the dominant factor inhibiting succession. Burning is influential in the Precambrian Outcrop Community Types.

Succession to the Upland Forest Community Type in the study region is estimated to take *ca.* 170 years, which is 60 years longer than Dirschl's (1973) estimate for a comparable climax type to develop in the southern portion of the Peace-Athabasca delta.

The "climatic climax" tree species in the study region is *Picea glauca*, while "edaphic climax" species in the Bog Community Type and Precambrian Outcrop Community Types are *P. mariana* and *Pinus banksiana*, respectively.

Several prominent species, vegetation units, and seral pathways differ considerably from those reported earlier by Raup (1935) and Dirschl *et al.* (1974) for the Peace-Athabasca delta. These differences are the result of variations in sedimentation, site stability and age, the absence of one or more seral stages, and in the methods employed, and, hence, the results obtained. Of the five study areas investigated, the Egg Lake area has

most in common with the botanical patterns and trends described in Raup and Dirschl, followed in decreasing order by the Chilaway Snye, Lake Athabasca Marsh, Revillon Coupé, and Nuphar Lake study areas. This thesis has attempted to describe the wide spectrum of botanical variation found in the study region, without assessing the relative extents of different community types or relative frequencies of seral sequences. Such work remains to be done over much of the Peace-Athabasca delta before a true appreciation of its complexity and dynamics can be gained. Similarly, more work should be done on retrogressive changes caused by flooding.

The flora and vegetation of the study region in 1970-72 were in dynamic equilibrium with the total environmental complex, including its variable hydrologic regime. Any imposed stabilization of the regional hydrology will drastically alter this dynamic balance, by favouring ombrotrophic and oligotrophic conditions and reducing minerotrophic and eutrophic conditions, thus promoting abnormally rapid senescence of the delta.

Since virtually all of the study region and much of the larger delta fall within the boundaries of Wood Buffalo National Park, Parks Canada must, to enforce its mandate, be careful to insure that "normal hydrologies" of the Peace and Athabasca Rivers are not changed enough to upset this balance.

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Appendix 1. Subjective scales for making semi-quantitative and qualitative estimates based on modified Braun-Blanquet scales (1932).

Cover

Cover Class	Range of each Cover Class (%)	Mid-point of each Cover Class (%) used for calculation
+	< 1	0.5
1	1 - 5	3.0
2	5 - 15	10.0
3	15 - 25	20.0
4	25 - 50	37.5
5	50 - 75	67.5
6	75 - 95	85.0
7	95 - 100	97.5

Dispersion

Dispersion Class	Pattern Type
1	Regular
2	Semi-regular
3	Random
4	Semi-contagious
5	Contagious

Vitality

1. plants germinating, but dying soon after without reproducing
2. plants lingering after germination, but not reproducing
3. plants reproducing only vegetatively
4. plants reproducing rather feebly by sexual methods
5. plants reproducing very well by sexual methods

Appendix 2. Physical properties of soil samples taken from zones at each site in the study region. Only the 15-30 cm sampling interval is represented.

Community Type[a]	Study Area[b]	Study Site	Zone	Sampling Date	Texture (%)[c] S	Si	C	S/C Ratio[d]	Texture Class[e]	GFM[f] (%)	Soil Moisture (%)[g] FC	PWP	AW	Organic Matter[h] Mean (Range)
Herb	RC	3	22	27/IX/71	77	15	8	9.6	SL	36	33	5	28	3.0(0)
Immature		4	42	18/IX/71	49	41	10	4.9	L,SL	31	33	6	27	.
Marsh			43		52	38	10	5.2	L,SL	34	31	7	24	4.0(0)[i]
			44		52	38	10	5.2	L,SL	34	33	6	27	.
	LAM	1	59	6/X/71	60	20	20	3.0	SCL,SL	34	36	11	25	3.0(0)
	CS	3	95	4/IX/71	52	20	28	1.9	SCL	67	54	24	30	4.0(0)[i]
Average					57	29	14	5.0		39	37	10	27	3.5(3.0-4.0)
Wet	EL	1	104	13/IX/71	—[j]	—	—	—	O	225	68	33	35	.
Meadow			105		—	—	—	—	O	214	70	34	36	
		2	114	29/IX/71	—	—	—	—	O	245	69	34	35	7.5(3.0-9.0)
			115		—	—	—	—	O	252	65	30	35	9.0(0)
			116		50	40	10	5.0	SL	114	35	13	22	5.5(5.0-6.0)
		3	122	17/IX/71	—	—	—	—	O	300	---[k]	---	---	.
			123		—	—	—	—	O	335	55	30	25	.
			124		—	—	—	—	O	243	50	20	30	.
			125		49	34	17	2.9	L	63	45	16	29	.
Average					50	37	13	4.0		221	57	26	31	7.3(3.0-9.0)
Meadow	CS	1	79	3/IX/71	45	12	43	1.0	SC,C	44	42	23	19	3.5(3.0-4.0)
			80		41	13	46	0.9	C	44	42	21	21	3.0(0)
			81		50	16	34	1.5	SCL	52	40	21	19	4.0(3.0-5.0)
		2	88	3/IX/71	50	12	38	1.3	SC	35	45	19	26	.
			89		50	14	36	1.4	SC	43	41	20	21	.
			90		50	19	31	1.6	SCL	45	44	25	19	.
		3	96	4/IX/71	54	18	28	1.9	SCL	58	52	25	27	.
			97		46	16	38	1.2	SC	52	48	25	23	.
			98		41	38	21	2.0	L	49	50	26	24	.
			99		45	16	39	1.2	CL,SC	46	47	20	27	.
	EL	1	106	13/IX/71	—	—	—	—	O	165	75	52	23	.
			107		50	32	18	2.8	L	93	34	17	17	.
		3	126	17/IX/71	52	31	17	3.1	L,SL	66	59	21	38	.
Average					48	20	32	1.7		61	47	24	23	3.5(3.0-5.0)
Fen	CS	3	100	4/IX/71	53	22	25	2.1	SCL	34	19	9	10	.
	EL	1	108	13/IX/71	53	33	14	3.8	SL	94	45	19	26	.
			109		52	34	14	3.7	SL,L	53	29	13	16	.
			110		63	25	12	5.2	SL	33	32	14	18	.
		2	117	29/IX/71	57	36	7	8.1	SL	34	36	13	23	4.8(3.0-7.0)
			118		49	35	16	3.1	L	44	38	18	20	5.0(3.0-9.0)
		3	127	17/IX/71	51	30	19	2.7	L	61	51	19	32	.
			128		54	35	11	4.9	SL	52	45	17	28	.
Average					54	31	15	4.2		51	37	15	22	4.9(3.0-9.0)
Marsh	LAM	1	53	6/X/71	48	35	17	2.8	L	38	36	11	25	3.0(0)
			54		48	34	18	2.7	L	39	34	10	24	3.0(0)
			55		52	36	12	4.3	SL,L	33	30	8	22	3.0(0)
			56		46	30	24	1.9	L	36	34	11	23	3.0(0)
			57		48	34	18	2.7	L	43	38	13	25	3.0(0)
		2	61	6/X/61	42	30	28	1.5	CL	35	36	10	26	.
			62		47	41	12	3.9	L	33	38	11	27	.
			63		48	36	16	3.0	L	32	37	11	26	.
			64		50	34	16	3.1	L	34	38	10	28	.
			65		49	27	24	2.0	SCL	38	36	11	25	.
			66		53	35	12	4.4	SL	36	30	8	22	.
		3	69	6/X/71	50	32	18	2.8	L	33	34	11	23	.
			70		55	31	14	3.9	SL	32	30	9	21	.
			71		55	31	14	3.9	SL	27	30	9	21	.
			72		59	27	14	4.2	SL	27	28	8	20	.
			73		53	33	14	3.8	SL	30	32	8	24	.
			74		48	33	19	2.5	L	34	35	13	22	.
			75		52	27	21	2.5	SCL	30	29	8	21	.
	CS	1	77	3/IX/71	39	17	44	0.9	C	41	38	19	19	3.0(0)
			78		41	15	44	0.9	C	40	39	22	17	3.0(0)
		2	86	3/IX/71	46	19	35	1.3	SC,SCL	35	41	19	22	.
			87		46	16	38	1.2	SC	32	38	19	19	.
Average					49	30	21	2.7		34	35	12	23	3.0(0)
Shrub	LAM	1	50	6/X/71	43	34	23	1.9	L	40	40	10	30	3.0(0)
Immature			51		48	34	18	2.7	L	34	35	10	25	3.0(0)
Marsh			52		46	36	18	2.6	L	34	36	11	25	3.0(0)
			58		46	34	20	2.3	L	33	36	11	25	3.0(0)
		2	60	6/X/71	42	43	15	2.8	L	34	36	10	26	.
		3	67	6/X/71	50	34	16	3.1	L	36	35	10	25	.
			68		46	36	18	2.6	L	36	32	10	22	.
Average					46	36	18	2.6		35	35	10	25	3.0(0)
Levee	RC	1	1	27/IX/71	58	34	8	7.2	SL	24	14	4	10	.
Herb			3		60	29	11	5.4	SL	19	19	6	13	.
			4		66	27	7	9.4	SL	18	12	4	8	.
			5		76	18	6	12.7	SL,LS	25	16	3	13	.
			6		95	3	2	47.5	S	23	15	1	14	.
			7		93	4	3	31.0	S	21	14	2	12	.
		2	12	27/IX/71	76	16	8	9.5	SL	22	18	5	13	.
			13		88	8	4	22.0	S	19	15	5	10	.
			14		94	2	4	23.5	S	28	20	2	18	.
			15		66	22	12	5.5	SL	25	25	6	19	0.5(0)
		3	16	27/IX/71	85	7	8	10.6	LS	21	31	5	26	3.0(0)
			17		72	23	5	14.4	SL	27	34	11	23	3.0(0)
			18		69	26	5	13.8	SL	27	21	6	15	3.0(0)
			19		61	31	8	7.6	SL	20	17	4	13	3.0(0)

Appendix 2. (Cont'd)

Community Type	Study Area	Study Site	Zone	Sampling Date	Texture (%)			S/C Ratio	Texture Class	GFM (%)	Soil Moisture (%)			Organic Matter Mean (Range)
					S	Si	C				FC	PWP	AW	
			20		54	37	9	6.0	SL	32	23	5	18	3.0(0)
			21		52	38	10	5.2	SL	24	28	5	23	3.0(0)
			23		78	16	6	13.0	LS	28	26	4	22	.
			24		54	36	10	5.4	SL	31	26	5	21	.
			25		56	37	7	8.0	SL	30	27	4	23	3.0(0)
Average					71	22	7	13.6		24	21	5	16	3.0(0.5-3.0)
Swale Shrub	RC	4	40	18/IX/71	58	30	12	4.8	SL	16	19	5	14	.
			41		46	41	13	3.5	L	38	38	10	28	.
			45		48	42	10	4.8	L,SL	33	37	7	30	4.0(0)[i]
Average					50	38	12	4.4		29	31	7	24	4.0(0)
Levee Shrub	RC	1	2	27/IX/71	49	43	8	6.1	SL	20	21	4	17	3.0(0)
			8		51	40	9	5.7	SL	20	25	7	18	.
			9		53	39	8	6.6	SL	22	27	6	21	.
		3	26	27/IX/71	69	22	9	7.7	SL	21	18	5	13	3.0(0)
			27		63	27	10	6.3	SL	16	20	5	15	3.0(0)
			28		52	31	17	3.1	SL	24	23	6	17	3.0(0)
			29		54	33	13	4.2	SL	19	20	4	16	3.0(0)
		4	34	18/IX/71	70	22	8	8.8	SL	28	17	4	13	.
			35		60	32	8	7.5	SL	15	21	5	16	.
			39		52	34	14	3.7	SL,L	29	34	9	25	.
			46		60	29	11	5.4	SL	23	27	5	22	.
			47		49	37	14	3.5	L	37	36	12	24	.
Average					57	32	11	5.7		23	24	6	18	3.0(0)
Levee Tree	RC	1	10	27/IX/71	64	27	9	7.1	SL	16	16	4	12	.
			11		60	32	8	7.5	SL	17	12	4	8	.
		3	30	27/IX/71	60	32	8	7.5	SL	19	21	6	15	3.0(0)
			31		54	33	13	4.2	SL	16	21	4	17	3.0(0)
			32		48	34	18	2.7	L	14	33	11	22	3.0(0)
		4	36	18/IX/71	56	36	8	7.0	SL	16	18	4	14	.
			37		47	37	16	2.9	L	12	15	3	12	.
			48		63	29	8	7.9	SL	18	16	8	8	.
Average					56	33	11	5.8		16	19	6	13	3.0(0)
Upland Forest	RC	3	33	27/IX/71	54	34	12	4.5	SL	29	27	9	18	4.0(3.0-5.0)
		4	38	18/IX/71	53	39	8	6.6	SL	16	18	7	11	6.8(2.0-9.0)
			49		56	36	8	7.0	SL	15	17	10	7	.
	CS	1	84	3/IX/71	62	29	9	6.9	SL	9	14	4	10	3.2(2.0-4.0)
		2	93	3/IX/71	54	18	28	1.9	SCL	22	22	5	17	.
		3	102	4/IX/71	54	22	24	2.2	SCL	12	24	4	20	.
	EL	1	111	13/IX/71	53	37	10	5.3	SL	34	27	10	17	.
		2	119	29/IX/71	56	36	8	7.0	SL	35	24	15	9	4.5(3.0-7.0)
			120		58	34	8	7.2	SL	28	20	8	12	5.5(3.0-9.0)
		3	129	17/IX/71	50	35	15	3.3	L	48	40	12	28	.
			130		56	34	10	5.6	SL	27	30	12	18	.
	NL	1	137	19/VIII/71	44	10	46	1.0	C	19	27	9	18	4.8(3.0-8.0)
		2	146	19/VIII/71	50	19	31	1.6	SCL	23	30	10	20	.
		3	155	20/VIII/71	52	20	28	1.9	SCL	24	30	10	20	.
Average					54	29	17	4.4		24	25	9	16	4.8(2.0-9.0)
Moist Lowland Forest	CS	1	82	3/IX/71	44	11	45	1.0	C	63	50	23	27	3.0(0)
			83		49	11	40	1.2	SC	21	17	8	9	2.5(2.0-3.0)
		2	91	3/IX/71	54	10	36	1.5	SC	37	35	23	12	.
			92		55	15	30	1.8	SCL	26	24	14	10	.
		3	101	4/IX/71	54	14	32	1.7	SCL	26	34	16	18	.
Average					51	12	37	1.4		35	32	17	15	2.8(2.0-3.0)
Wet Lowland Forest	NL	2	145	19/VIII/71	52	9	39	1.3	SC	26	39	18	21	.
		3	153	20/VIII/71	46	12	42	1.1	SC	65	67	39	28	4.0(0)[i]
			154		26	25	49	0.5	C	39	39	15	24	.
Average					41	16	43	1.0		43	43	24	24	4.0(0)
Bog	NL	1	132	19/VIII/71	.	.	.	.	O	889	122	51	71	10.0(0)
			133		.	.	.	.	O	1160	135	114	21	10.0(0)
			134		.	.	.	.	O	1810	148	124	24	10.0(0)
			135		.	.	.	.	O	1120	116	94	22	10.0(0)
			136		.	.	.	.	O	530	117	68	49	10.0(0)
		2	139	19/VIII/71	.	.	.	.	O	---	---	---	---	.
			140		.	.	.	.	O	722	125	96	29	.
			141		.	.	.	.	O	1140	164	126	38	.
			142		.	.	.	.	O	1490	148	125	23	.
			143		.	.	.	.	O	582	68	43	25	.
			144		.	.	.	.	O	314	100	69	31	.
		3	148	20/VIII/71	.	.	.	.	O	546	125	110	15	.
			149		.	.	.	.	O	765	200	118	82	.
			150		.	.	.	.	O	1440	177	115	62	.
			151		.	.	.	.	O	1100	158	100	58	.
			152		.	.	.	.	O	606	140	94	46	.
Average					.	.	.	.		948	136	96	40	10.0(0)
Precambrian Outcrop	RC	Main[l] Camp		13/VI/71	58	40	2	29.0	SL	10	16	8	8	4.0(0)

[a] No sampling conducted in the Algal and Vascular Aquatic Community Types.
[b] EL: Egg Lake, RC: Revillon Coupe, LAM: Lake Athabasca Marsh, CS: Chilaway Snye, NL: Nuphar Lake.
[c] S: Sand, Si: Silt, C: Clay.
[d] S/C: Sand/Clay.
[e] O: Organic, SL: Sandy Loam, L: Loam, SCL: Sandy Clay Loam, SC: Sandy Clay, C: Clay, CL: Clay Loam, LS: Loamy Sand, S: Sand.
[f] Gravimetric Field Moisture.
[g] FC: Field Capacity, PWP: Permanent Wilting Point, AW: Available Water.
[h] Data converted from qualitative scale and represent solum intervals (0-15, 15-30, 30-61, 61-91 cm). Sampling conducted on dates given in Appendix 3.
[i] Data represent one sample for all intervals.
[j] Organic.
[k] Samples lost or insufficient for analysis.
[l] Camp located between sites # 2,3 of the EL study area.

Appendix 3. Chemical properties of soil samples taken from profile intervals (0-15, 15-30, 30-61, 61-91 cm) of selected zones at certain sites in the study region.

Community Type	Study Area[a]	Study Site	Zone	Sampling Date	Nitrogen[b] (kg/ha)	Phosphorus[c] (kg/ha)	Potassium[d] (kg/ha)	Sodium[e]	pH	Conductivity (mmhos/cm)	Sulphate[e]	Free Calcium Carbonate[e]
Herb	RC	2	22	5/VII/71	2.2(0)[f]	4.9(4.5-5.6)	239(213-269)	3.0(0)	7.5(0)	0.6(0.6-0.7)	0.5(0)	10.0(0)
Immature		4	43	18/IX/71	2.2(0)	5.6(0)	314(0)	3.0(0)	7.6(0)	1.5(0)	2.0(0)	8.0(0)
Marsh	LAM	1	59	10/X/71	2.2(0)	0.4(0-1.1)	400(381-415)	3.0(0)	7.6(0)	0.6(0)	0.5(0)	10.0(0)
	CS	3	95[g]	4/IX/71	5.6(0)	5.6(0)	525(0)	4.0(0)	7.2(0)	2.7(0)	8.0(0)	0.5(0)
Average					3.0(2.2-5.6)	4.1(0-5.6)	370(213-525)	3.2(3.0-4.0)	7.5(7.2-7.6)	1.4(0.6-2.7)	2.8(0.5-8.0)	7.1(0.5-10.0)
Wet Meadow	EL	2	115	7/VII/71	1.8(1.1-2.2)	5.2(0-15.7)	206(134-286)	4.3(3.0-5.0)	7.1(6.7-7.3)	0.8(0.8-0.9)	0.5(0)	0.5(0)
Meadow	CS	1	79	18/VI/71	1.6(1.1-2.2)	7.3(0-14.6)	563(560-566)	4.0(3.0-5.0)	5.9(5.5-6.3)	0.8(0.7-1.0)	0.5(0)	1.8(0.5-3.0)
			80		1.1(0)	1.6(1.1-2.2)	535(527-544)	4.0(3.0-5.0)	6.5(6.3-6.7)	0.8(0.6-1.0)	0.5(0)	2.2(0.5-4.0)
			81		3.4(2.2-4.5)	3.6(0.5-6.7)	446(398-493)	4.0(3.0-5.0)	6.2(5.3-7.2)	1.2(0.6-1.8)	1.2(0.5-2.0)	0.5(0)
Average					2.0(1.1-4.5)	4.2(0-14.6)	515(398-566)	4.0(3.0-5.0)	6.2(5.3-7.2)	0.9(0.6-1.8)	0.7(0.5-2.0)	1.5(0.5-4.0)
Fen	EL	2	117	7/VII/71	4.1(1.1-9.0)	4.9(1.1-12.6)	161(114-213)	4.3(3.0-5.0)	7.5(6.8-7.9)	0.9(0.8-1.1)	1.0(0.5-2.0)	6.7(2.0-10.0)
			118		3.0(2.2-4.5)	6.1(0-16.2)	213(140-275)	3.7(3.0-4.0)	6.7(5.8-7.4)	0.9(0.7-1.0)	0.5(0)	5.5(0.5-9.0)
Average					3.6(1.1-9.0)	5.5(0-16.2)	187(114-275)	4.0(3.0-5.0)	7.1(5.8-7.9)	0.9(0.7-1.1)	0.8(0.5-2.0)	6.1(0.5-10.0)
Marsh	LAM	1	53	10/X/71	1.8(1.1-2.2)	2.2(0)	351(325-392)	3.0(0)	7.5(7.5-7.6)	0.5(0)	0.5(0)	9.3(8.0-10.0)
			54		2.2(0)	0.6(0)	334(303-370)	3.0(0)	7.6(0)	0.6(0.6-0.7)	0.5(0)	7.7(7.0-8.0)
			55		1.8(1.1-2.2)	0.7(0-1.1)	305(286-331)	3.0(0)	7.6(7.4-7.8)	0.7(0.6-0.7)	0.5(0)	7.0(2.0-9.0)
			56		2.2(1.1-3.4)	0.4(0-1.1)	348(292-443)	3.0(0)	7.6(7.5-7.6)	0.7(0.6-0.8)	0.5(0)	9.7(9.0-10.0)
			57		1.5(1.1-2.2)	0.6(0)	351(342-364)	2.7(2.0-3.0)	7.7(7.7-7.8)	0.8(0.7-1.0)	0.5(0)	5.3(5.0-6.0)
	CS	1	77	18/VI/71	1.1(0)	3.4(2.2-4.5)	562(549-575)	3.5(3.0-4.0)	6.7(6.6-6.8)	0.6(0.5-0.7)	0.5(0)	3.5(3.0-4.0)
			78		1.1(0)	5.0(2.2-7.8)	530(510-549)	3.0(0)	6.2(5.8-6.5)	0.7(0.6-0.8)	0.5(0)	1.8(0.5-3.0)
Average					1.7(1.1-3.4)	1.8(0-7.8)	397(266-575)	3.0(2.0-4.0)	7.3(5.8-7.8)	0.7(0.5-1.0)	0.5(0)	6.3(0.5-10.0)
Shrub	LAM	1	50	10/X/71	2.2(0)	1.5(1.1-2.2)	423(420-429)	3.0(0)	7.2(7.2-7.3)	0.6(0)	1.0(0.5-2.0)	8.7(6.0-10.0)
Immature			51		7.5(6.7-9.0)	2.6(1.1-3.4)	387(364-420)	3.0(0)	7.2(7.1-7.2)	0.9(0.8-0.9)	0.5(0)	10.0(0)
Marsh			52		1.5(1.1-2.2)	0.8(0.6-1.1)	379(359-404)	3.0(0)	7.9(7.8-7.9)	0.4(0.4-0.5)	0.5(0)	10.0(0)
			58		1.8(1.1-2.2)	1.1(0)	383(376-392)	3.0(0)	7.6(7.6-7.7)	0.7(0.6-0.8)	1.0(0.5-2.0)	10.0(0)
Average					3.2(1.1-9.0)	1.5(0.6-3.4)	393(359-429)	3.0(0)	7.5(7.1-7.9)	0.6(0.4-0.9)	0.8(0.5-2.0)	9.7(6.0-10.0)
Levee	RC	2	15	5/VII/71	1.1(0)	1.1(0)	176(162-185)	2.0(0)	7.0(7.0-7.1)	0.6(0.6-0.7)	0.5(0)	9.0(8.0-10.0)
Herb		3	17	5/VII/71	1.5(1.1-2.2)	2.6(1.1-5.6)	196(195-207)	2.0(0)	7.0(7.0-7.1)	1.2(0.8-1.8)	2.2(0.5-4.0)	9.0(8.0-10.0)
			18		1.5(0-3.4)	2.2(1.1-3.4)	176(162-185)	2.0(0)	7.3(7.3-7.4)	0.8(0.6-1.0)	0.5(0)	10.0(0)
			19		1.5(1.1-2.2)	0.7(0-1.1)	207(196-219)	2.0(0)	7.7(7.7-7.8)	1.2(0.7-1.7)	1.8(0.5-3.0)	10.0(0)
			20		1.1(0)	1.5(1.1-2.2)	211(196-219)	2.0(0)	7.1(7.0-7.1)	1.3(0.7-1.8)	3.7(3.0-4.0)	10.0(0)
			21		1.1(0)	3.4(2.2-4.5)	235(216-274)	2.0(0)	7.2(0)	0.5(0.4-0.6)	0.5(0)	10.0(0)
			25		3.7(1.1-7.8)	2.2(0)	351(252-544)	2.3(2.0-3.0)	7.2(0)	2.5(2.4-2.5)	8.0(0)	10.0(0)
Average					1.6(0-7.8)	2.0(0-5.6)	222(162-544)	2.0(2.0-3.0)	7.2(7.0-7.8)	1.2(0.4-2.5)	2.5(0.5-4.0)	9.7(8.0-10.0)
Swale Shrub	RC	4	45[g]	18/IX/71	3.4(0)	5.6(0)	231(0)	3.0(0)	7.6(0)	1.4(0)	2.0(0)	9.0(0)
Levee	RC	1	2	21/VI/71	1.5(1.1-2.2)	0.7(0-1.1)	383(263-622)	2.0(0)	7.6(7.5-7.8)	0.7(0.5-1.1)	1.0(0.5-2.0)	10.0(0)
Shrub		3	26	5/VII/71	2.2(1.1-4.5)	2.2(1.1-4.5)	273(252-308)	2.0(0)	7.1(7.0-7.1)	0.9(0.5-1.3)	1.7(0.5-4.0)	10.0(0)
			28		1.1(0)	23.5(2.2-63.9)	256(213-320)	2.7(2.0-3.0)	7.1(7.1-7.2)	1.2(0.7-2.1)	1.7(0.5-4.0)	10.0(0)
			29		1.1(0)	25.8(2.2-71.7)	336(250-454)	2.0(0)	7.2(7.0-7.3)	0.6(0)	0.5(0)	10.0(0)
Average					1.5(1.1-4.5)	13.0(0-71.7)	312(213-622)	2.2(2.0-3.0)	7.2(7.0-7.8)	0.8(0.5-2.1)	1.2(0.5-4.0)	10.0(0)
Levee	RC	3	30	5/VII/71	1.1(0)	4.5(2.2-7.8)	278(230-341)	2.7(2.0-4.0)	7.2(7.0-7.4)	0.9(0.5-1.6)	1.7(0.5-4.0)	10.0(0)
Tree			31		1.5(1.1-2.2)	0.7(0-1.1)	318(258-359)	1.7(0-3.0)	7.7(7.6-7.8)	0.5(0)	0.5(0)	10.0(0)
			32		2.6(2.2-3.4)	2.6(0-6.7)	420(370-516)	2.7(2.0-4.0)	7.2(7.1-7.2)	0.8(0.6-1.0)	0.5(0)	7.3(7.0-8.0)
Average					1.7(1.1-3.4)	2.6(0-7.8)	339(230-516)	2.4(0-4.0)	7.4(7.0-7.8)	0.7(0.5-1.6)	0.9(0.5-4.0)	9.1(7.0-10.0)
Upland	RC	3	33	5/VII/71	1.5(1.1-2.2)	14.6(4.5-23.5)	356(303-392)	2.7(2.0-3.0)	7.4(6.8-7.7)	0.6(0.5-0.7)	0.5(0)	3.5(0.5-5.0)
Forest		4	38	25/VI/71	3.4(2.2-4.5)	14.2(0-42.6)	351(213-532)	4.0(2.0-6.0)	7.6(7.0-8.0)	2.6(0.5-3.9)	5.5(0.5-8.0)	6.2(0.5-10.0)
	CS	1	84	19/VI/71	0.4(0-1.1)	43.7(7.8-63.9)	284(106-454)	3.0(2.0-4.0)	7.5(7.0-8.3)	0.3(0.2-0.3)	0.5(0)	3.7(0.5-10.0)
	EL	2	119	7/VII/71	1.9(1.1-3.4)	7.5(1.1-19.1)	237(179-286)	3.0(0)	7.1(6.8-7.4)	0.9(0.6-1.5)	0.5(0)	9.3(8.0-10.0)
			120		1.5(1.1-2.2)	17.8(0-45.4)	277(174-331)	2.3(2.0-3.0)	7.8(7.0-8.3)	0.6(0.6-0.7)	0.5(0)	6.8(0.5-10.0)
	NL	1	137	19/VIII/71	1.1(0)	27.8(10.1-47.0)	330(246-404)	3.7(2.0-5.0)	5.8(5.6-6.2)	0.3(0.3-0.4)	0.5(0)	1.5(0.5-2.0)
Average					1.6(0-4.5)	20.1(0-63.9)	306(106-532)	3.1(2.0-6.0)	7.2(5.6-8.3)	0.9(0.2-3.9)	1.3(0.5-8.0)	5.2(0.5-10.0)
Moist Lowland	CS	1	82	18/VI/71	1.8(1.1-2.2)	9.4(9.0-10.1)	462(376-605)	3.7(3.0-4.0)	5.7(5.2-6.1)	0.7(0.6-0.8)	0.5(0)	0.5(0)
Forest			83	23/VI/71	1.1(0-2.2)	6.7(0-11.2)	334(151-684)	3.0(0)	6.4(5.8-7.1	0.4(0)	0.5(0)	4.2(0.5-10.0)
Average					1.4(0-2.2)	8.0(0-11.2)	398(151-684)	3.4(3.0-4.0)	6.0(5.2-7.1)	0.6(0.4-0.8)	0.5(0)	2.4(0.5-10.0)
WLF[h]	NL	3	153[g]	20/VIII/71	2.2(0)	14.6(0)	249(0)	4.0(0)	7.0(0)	0.9(0)	0.5(0)	0.5(0)
Bog	NL	1	132	19/VIII/71	6.7(5.6-7.8)	7.0(2.7-11.2)	92(84-101)	3.5(3.0-4.0)	5.2(5.0-5.5)	1.0(1.0-1.1)	6.0(5.0-7.0)	0.5(0)
			133		1.6(1.1-2.2)	6.2(2.4-10.1)	118(106-129)	3.0(0)	5.2(5.0-5.5)	0.6(0.5-0.8)	0.5(0)	0.5(0)
			134		1.1(0)	2.2(0)	80(73-86)	3.0(0)	5.3(5.0-5.6)	0.3(0)	0.5(0)	0.5(0)
			136		1.1(0)	4.0(3.4-4.5)	86(78-94)	3.0(0)	5.1(5.0-5.2)	0.5(0)	0.5(0)	0.5(0)
Average					2.6(1.1-7.8)	4.8(2.2-11.2)	94(73-129)	3.1(3.0-4.0)	5.2(5.0-5.6)	0.6(0.3-1.1)	1.9(0.5-7.0)	0.5(0)
Precambrian Outcrop	RC	Main[i] Camp		13/VI/71	2.2(1.1-3.4)	63.4(25.8-101)	241(95-387)	2.0(0)	5.2(4.9-5.5)	0.2(0.2-0.3)	0.5(0)	0.5(0)

[a] RC: Revillon Coupé, LAM: Lake Athabasca Marsh, CS: Chilaway Snye, EL: Egg Lake, NL: Nuphar Lake.

[b] Available nitrogen.

[c] Available phosphorus.

[d] Available potassium.

[e] Data converted using digital conversion scale (See p.23).

[f] Mean (range).

[g] Data represent one sample for all profile intervals.

[h] Wet Lowland Forest.

[i] Camp located between sites #2,3 of the EL study area.

Appendix 4. Physical and chemical properties of samples taken from representative soil profiles at site #3 in the Revillon Coupé study area.

Zone	Soil[a] Type	Horizon	Organic[b] Matter	Texture (%)[c] S	Si	C	S/C[d] Ratio	Textural[e] Class	Available Nitrogen (kg/ha)	Available Phosphorus (kg/ha)	Available Potassium (kg/ha)	Sodium[b]	pH	Conductivity (mmhos/cm)	Sulphate[b]	Free Calcium[b] Carbonate
19	OR	surface	T	72	22	6	12.0	SL	2.2	1.1	219	L⁻	7.7	1.2	L⁻	H⁺
		Ck (S_1)f	L	50	44	6	5.6	SL	1.1	1.1	207	L⁻	7.7	1.7	L	H⁺
		(S_2)f	L	68	26	6	11.3	SL	1.1	0	196	L⁻	7.8	0.7	T	H⁺
27	OR	L	H⁺	--[g]	--	--	--	O	2.2	53.8	650	L⁻	7.0	1.1	L⁻	T
		Ck	L	61	31	8	7.6	SL	1.1	23.5	256	L	7.2	1.2	L⁻	H⁺
30	CR	LFH	H⁺	--	--	--	--	O	3.4	7.8	645	L⁻	6.8	1.4	L⁻	T
		Ck	L	57	33	10	5.7	SL	1.1	7.8	342	L⁻	7.1	0.5	T	H⁺
		Ahb	H⁺	--	--	--	--	O	3.4	1.1	118	M⁻	7.4	0.4	T	M⁺
		Ck_1	L	57	33	10	5.7	SL	1.1	3.4	263	L⁺	7.0	1.6	L⁺	H⁺
		Ahb_1	H⁺	--	--	--	--	O	—[h]	—	—	—	—	—	—	—
		Ck_2	L	50	35	15	3.3	L	1.1	2.2	230	L⁻	7.0	0.5	T	H⁺
		Ahb_2	H⁺	--	--	--	--	O	—	—	—	—	—	—	—	—
		Ck_3	L	59	31	10	5.9	SL	1.1	1.1	118	L⁻	7.4	0.5	T	H⁺
33	OGL	LFH	H⁺	--	--	--	--	O	2.2	40.4	521	L	5.8	0.7	T	T
		Ah	M⁻	60	27	13	4.6	SL	2.2	20.2	359	L⁻	7.4	0.7	T	T
		Aej	M⁻	54	34	12	4.5	SL	1.1	26.9	387	L	7.4	0.7	T	T
		Btj	L	54	34	12	4.5	SL	1.1	15.7	392	L	7.7	0.6	T	M⁻
		Ck	L	52	38	10	5.2	SL	1.1	4.5	303	L	7.7	0.5	T	M⁻

[a] OR: Orthic Regosol, CR: Cumulic Regosol, OGL: Orthic Gray Luvisol.
[b] T: Trace, L: Low, H: High, M: Medium.
[c] S: Sand, Si: Silt, C: Clay.
[d] S/C: Sand/Clay
[e] SL: Sandy Loam, O: Organic Matter.
[f] S_1: Sand Layer 1, S_2: Sandy Layer 2.
[g] Organic Matter.
[h] See Ahb.

Appendix 5. Physical and chemical properties of samples taken from representative soil profiles at site #1 in the Lake Athabasca Marsh study area.

Zone	Soil[a] Type	Horizon	Organic[b] Matter	Texture (%)[c] S	Si	C	S/C[d] Ratio	Textural[e] Class	Available Nitrogen (kg/ha)	Available Phosphorus (kg/ha)	Available Potassium (kg/ha)	Sodium[b]	pH	Conductivity (mmhos/cm)	Sulphate[b]	Free Calcium[b] Carbonate
51	GR	Cg	L	48	34	18	2.7	L	7.8	2.2	370	L	7.2	0.9	T	H+
		Cg_1	L	48	33	19	2.5	L	6.7	3.4	420	L	7.1	0.8	T	H+
53	GR	L,H	H+	--[f]	--	--	--	O	2.2	2.2	376	L	7.4	0.6	T	H+
		Ah	L	48	35	17	2.8	L	2.2	2.2	336	L	7.5	0.5	T	H+
		Cg	L	50	33	17	2.9	L	2.2	2.2	325	L	7.5	0.5	T	H+
		Cg_1	L	50	32	18	2.8	L	1.1	2.2	392	L	7.6	0.5	T	H−
56	GR	L,H	H+	--	--	--	--	O	2.2	1.1	611	L	7.6	0.7	T	H
		Cg	L	52	28	20	2.6	L	2.2	0.4	348	L	7.6	0.7	T	H+

[a] GR: Gleyed Regosol.
[b] L: Low, H: High, T: Trace.
[c] S: Sand, Si: Silt, C: Clay.
[d] S/C: Sand/Clay.
[e] L: Loam, O: Organic.
[f] Organic Matter.

Appendix 6. Physical and chemical properties of samples taken from representative soil profiles at site #1 in the Chilaway Snye study area.

Zone	Soil[a] Type	Horizon	Organic[b] Matter	Texture (%)[c] S	Si	C	S/C[d] Ratio	Textural[e] Class	Available Nitrogen (kg/ha)	Available Phosphorus (kg/ha)	Available Potassium (kg/ha)	Sodium[b]	pH	Conductivity (mmhos/cm)	Sulphate[b]	Free Calcium[b] Carbonate
78	RG	LFH	H+	--[f]	--	--	--	O	6.7	44.8	454	L	6.0	0.7	T	T
		Ah	L	41	14	45	0.9	C	1.1	7.8	510	L	5.8	0.6	T	T
		Cg	L	44	16	40	1.1	C	1.1	2.2	549	L	6.5	0.8	T	L
80	RG	LFH	H+	--	--	--	--	O	3.4	22.4	387	L	6.0	0.8	T	T
		Ah	L	42	14	44	1.0	C	1.1	2.2	527	L	6.3	0.6	T	T
		Cg	L	41	13	46	0.9	C	1.1	1.1	544	M-	6.7	1.0	T	L+
83	OG	LFH	H+	--	--	--	--	O	5.6	77.4	549	L-	5.8	0.8	T	T
		Ah	L	46	8	46	1.0	SC	3.4	14.6	734	L	5.6	0.5	T	T
		Aejg	L	49	11	40	1.2	SC	2.2	7.8	633	L	5.9	0.4	T	T
		Bgtj	L-	72	17	11	6.6	SL	1.1	7.8	168	L	6.3	0.4	T	L-
		Bgtj1	L-	78	17	5	15.6	LS	1.1	9.0	134	L-	6.4	0.4	T	L-
		Cca	L-	68	9	23	3.0	SCL	0	0	168	L	7.1	0.4	T	H+
84	FG	LFH	H+	--	--	--	--	O	5.6	59.4	617	L-	6.3	0.6	T	T
		Ah	L+	58	34	8	7.2	SL	1.1	63.9	454	L	7.1	0.3	T	T
		Bgf	L	73	21	6	12.2	SL	0	59.4	292	L+	7.0	0.2	T	T
		Ck	L-	89	8	3	29.7	S	0	7.8	106	L-	8.3	0.3	T	H+

a RG: Rego Gleysol, OG: Orthic Gleysol, FG: Fera Gle ysol.
b H: High, L: Low, T: Trace.
c S: Sand, Si: Silt, C: Clay.
d S/C: Sand/Clay.
e O: Organic Matter, C: Clay, SC: Sandy Clay, SL: Sa ndy Loam, LS: Loamy Sand, SCL: Sandy Clay Loam, S: Sand.
f Organic Matter.

Appendix 7. Physical and chemical properties of samples taken from representative soil profiles at site #2 in the Egg Lake study area.

Zone	Soil[a] Type	Horizon	Organic[b] Matter	Texture (%)[c] S	Si	C	S/C[d] Ratio	Textural[e] Class	Available Nitrogen (kg/ha)	Available Phosphorus (kg/ha)	Available Potassium (kg/ha)	Sodium[b]	pH	Conductivity (mmhos/cm)	Sulphate[b]	Free Calcium[b] Carbonate
118	OG	LFH	H+	--[f]	--	--	--	O	3.4	96.4	628	L	6.1	1.0	T	T
		Ah	H	49	35	16	3.1	L	3.4	25.8	235	L+	5.5	1.1	T	T
		Aeg	L+	57	34	9	6.3	SL	1.1	6.7	314	L	6.2	0.8	T	T
		Ahb	H+	--	--	--	--	O	—[g]	—	—	—	—	—	—	—
		Aeg_1	M−	h	h	h	h	h	1.1	5.6	106	M−	6.4	1.1	T	T
		Ahb_1	H+	--	--	--	--	O	—	—	—	—	—	—	—	—
		Aeg_2	h	h	h	h	h	h	h	h	h	h	h	h	h	h
		Bg	L+	54	32	14	3.9	SL	2.2	0	185	L+	6.9	0.8	T	M+
		Ahb_2	H	--	--	--	--	O	—	—	—	—	—	—	—	—
		Aeg_3	L	h	h	h	h	h	2.2	0	129	L+	7.4	0.7	T	M+
		Bg_1	L	i	i	i	i	i	4.5	0	224	M−	7.4	0.7	T	H
120	COGL	LFH	H+	--	--	--	--	O	3.4	95.3	521	L	6.6	0.8	T	T
		Ah	H	70	24	6	11.7	SL	1.1	65.0	426	L−	6.7	0.6	T	T
		Ae	M−	58	34	8	7.2	SL	1.1	25.8	230	M	7.2	0.8	T	T
		Btj	L+	56	34	10	5.6	SL	3.4	15.7	252	L−	8.0	0.5	T	H
		Bt	L	54	34	12	4.5	SL	0	1.1	409	L	8.2	0.6	T	H+
		Ahb	H+	--	--	--	--	O	—	—	—	—	—	—	—	—
		Ck	L	70	24	6	11.7	SL	1.1	0	174	L	8.3	0.6	T	H+
		Ahb_1	H+	--	--	--	--	O	—	—	—	—	—	—	—	—
		Ck_1	j	j	j	j	j	j	j	j	j	j	j	j	j	j
		Ahb_2	H+	--	--	--	--	O	—	—	—	—	—	—	—	—
		Ck_2	j	j	j	j	j	j	j	j	j	j	j	j	j	j
		Ahb_3	H+	--	--	--	--	O	—	—	—	—	—	—	—	—
		Ck_3	j	j	j	j	j	j	j	j	j	j	j	j	j	j

a OG: Orthic Gleysol, COGL: Cumulic Orthic Gray Luvisol.
b H: High, L: Low, M: Medium, T: Trace.
c S: Sand, Si: Silt, C: Clay.
d S/C: Sand/Clay.
e O: Organic Matter, L: Loam, SL: Sandy Loam.
f Organic Matter.
g Samples lost or not taken.
h See previous Aeg.
i See Bg.
j See Ck.

Appendix 8. Physical and chemical properties of samples taken from representative soil profiles at site #1 in the Nuphar Lake study area.

Zone	Soil[a] Type	Horizon	Organic[b] Matter	Texture (5)[c] S	Si	C	S/C[d] Ratio	Textural[e] Class	Available Nitrogen (kg/ha)	Available Phosphorus (kg/ha)	Available Potassium (kg/ha)	Sodium[b]	pH	Conductivity (mmhos/cm)	Sulphate[b]	Free Calcium[b] Carbonate
133	O	surface	H+	--[f]	--	--	--	O	3.4	11.2	106	L	5.6	1.1	T	T
		SS_1[g]	H+	--	--	--	--	O	2.2	10.1	106	L	5.5	0.8	T	T
		SS_2	H+	--	--	--	--	O	1.1	2.2	129	L	5.0	0.5	T	T
		SS_3	H+	--	--	--	--	O	_[h]	_	_	_	_	_	_	_
		SS_4	i	i	i	i	i	i	i	i	i	i	i	i	i	i
137	OGL	L-H	H+	--	--	--	--	O	3.4	42.6	493	L⁻	6.5	0.5	T	T
		Ah	H+	_	_	_	_	L	1.1	100.9	633	L⁻	5.9	0.7	T	T
		Ae	L	60	22	18	3.3	SL	1.1	29.2	207	L⁻	6.4	0.3	T	T
		AB	L	58	24	18	3.2	SL	1.1	11.2	174	L⁻	6.3	0.3	T	L⁻
		Bt	L⁻	44	10	46	1.0	C	1.1	12.3	406	M⁻	5.7	0.3	T	L⁻
		Bt_1	L⁻	46	18	36	1.3	SC	1.1	9.0	381	M⁻	5.6	0.3	T	L⁻
		Bt_2	L⁻	52	14	34	1.5	SCL	1.1	10.1	448	M⁻	5.4	0.3	T	L⁻
		C	L⁻	97	1	2	48.5	S	1.1	10.1	45	L⁻	5.8	0.3	T	T
		R	j	j	j	j	j	j	j	j	j	j	j	j	j	j

a O: Organic, OGL: Orthic Gray Luvisol.
b H: High, L: Low, M: Medium, T: Trace.
c S: Sand, Si: Silt, C: Clay.
d S/C: Sand/Clay.
e O: Organic, L: Loam, SL: Sandy Loam, C: Clay, SC: Sandy Clay, SCL: Sandy Clay Loam, S: Sand.
f Organic Matter.
g SS_{1-4}: Sub-Surface layers.
h Sample lost.
i No samples taken because of lake water.
j No samples taken because of Precambrian rock.

Appendix 9. Distribution relationships of species among community types in the study region. Designation of species groupings was based on 50% species occurrences within each group and 10% species occurrences in community types present outside the group.

Species	Community Type[a,b]														
	16	2	4	6	5	7	8	9	10	11	12	13	15	14	3
	16[c]	10	9	8	13	22	7	19	3	12	8	14	3	5	6
Tree Stratum: A	0.8	.	0.1	0.6	0.1	0.1	.	.	0.3	0.5	3.1	3.9	5.0	1.8	.
Larix laricina	32[d]	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Picea mariana	22	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Populus balsamifera	.	.	.	.	.	.	.	.	.	37	470	162	107	13	.
Alnus tenuifolia	3.9	.	.	.	.	.	.	.	.	51	415	48	279	.	.
Picea glauca	7.9	.	.	.	.	.	.	.	.	.	34	245	283	18	.
Populus tremuloides	.	.	.	.	.	.	.	.	.	.	.	138	42	88	.
Betula papyrifera	.	.	.	.	.	.	.	.	.	.	24	89	5.0	.	.
Salix scouleriana	.	.	.	.	.	.	.	.	.	.	.	1.4	.	36	.
S. bebbiana	.	.	9.9	304	.	6.9	.	.	.	67	27	132	.	320	.
S. arbusculoides	18	.	.	.	0.2	.	.	.	.	.	.	28	153	58	.
S. interior	.	.	.	.	.	.	.	.	125	.	.	.	.	.	.
Shrub Stratum: A	7.6	.	0.8	2.0	3.1	4.0	2.7	2.6	4.0	5.2	5.0	7.1	7.3	2.8	.
Myrica gale	174	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix pedicellaris	120	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chamaedaphne calyculata	98	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Betula glandulosa	75	.	.	.	.	.	.	.	.	.	.	.	.	.	.
B. pumila	58	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Larix laricina	56	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ledum groenlandicum	51	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Picea mariana	47	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Andromeda polifolia	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix pyrifolia	20	.	19	42	54	58	20	3.7	.	.	.	.	.	.	.
S. petiolaris	.	.	29	42	84	14	.	0.2	.	.	.	.	.	.	.
S. lutea	.	.	.	.	76	120	56	89	35	106	.	.	.	.	.
S. interior	.	.	.	.	.	117	137	143	134	157	.	.	.	.	.
S. lasiandra	.	.	.	.	1.3	.	2.7	3.4	.	16	.	.	.	.	.
Shepherdia canadensis	.	.	.	.	.	.	.	.	.	.	11	64	112	.	.
Rubus strigosus	.	.	.	.	.	.	.	.	.	.	16	22	0.7	.	.
Ribes oxyacanthoides	.	.	.	.	.	.	.	.	.	.	1.6	16	0.7	.	.
R. hudsonianum	.	.	.	0.5	.	.	.	.	.	.	0.2	0.1	5.0	.	.
Viburnum edule	.	.	.	.	.	.	.	.	.	.	38	107	.	.	.
Ribes triste	.	.	.	.	.	.	.	.	.	.	20	17	.	.	.
Amelanchier alnifolia	.	.	.	.	.	.	.	.	.	.	.	36	.	.	.
Symphoricarpos albus	.	.	.	.	.	.	.	.	.	.	.	4.7	.	.	.
Ribes lacustre	.	.	.	.	.	.	.	.	.	.	.	0.3	.	.	.
Salix arbusculoides	.	.	.	.	9.7	.	.	.	.	.	.	14	43	92	.
S. scouleriana	0.1	.	.	.	.	.	.	.	.	.	.	0.1	.	0.8	.
S. bebbiana	0.1	.	.	233	.	77	.	19	.	66	19	45	192	112	.
Alnus tenuifolia	31	.	.	0.2	.	11	.	.	410	409	102	22	234	.	.
Populus balsamifera	.	.	.	.	.	7.8	3.9	.	.	56	68	14	7.7	.	.
Salix serissima	16	.	9.9	19	0.6	.	.	.	.	.	.	.	0.7	75	.
Cornus stolonifera	.	.	.	0.2	.	.	.	3.3	.	42	313	90	.	.	.
Rosa acicularis	.	.	.	0.2	.	.	.	.	.	13	172	192	1.0	.	.
Picea glauca	3.9	.	.	.	.	0.1	.	.	.	.	.	36	219	1.0	.
Salix pseudomonticola	.	.	0.2	.	42	.	.	3.4	30	0.2	.	.	.	.	.
Populus tremuloides	.	.	.	.	0.2	2.4	.	.	.	.	.	11	.	33	.
Betula papyrifera	.	.	.	.	.	0.1	.	.	21	.	.	14	.	0.6	.
Salix glauca	0.1	.	.	7.9	.	.	.	.	.	.	.	.	0.7	.	.
Salix spp.	.	.	.	.	6.9	7.0	.	.	.	.	.	.	.	.	.
S. myrtillifolia	23[e]	.	.	.	.	.	.	.	.	.	.	.	60[e]	.	.
S. barklayi (?):f,g	14	.	.	.	.	.	.	.	.	.	.	.	5.0	.	.
Herb-Dwarf Shrub Stratum: A	23	7.2	21	21	19	31	15	10	15	11	7.6	25	30	12	8.7
Myrica gale	117	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ledum groenlandicum	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calla palustris	34	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chamaedaphne calyculata	29	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex diandra	27	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Larix laricina	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Betula pumila	16	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex limosa	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix pedicellaris	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Andromeda polifolia	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex disperma	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oxycoccus quadripetalus	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eriophorum angustifolium	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex paupercula	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Drosera rotundifolia	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Menyanthes trifoliata	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rubus chamaemorus	1.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex occidentalis	1.3	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Picea mariana	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex tenuiflora	0.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix serissima	0.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex brunnescens	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
C. lasiocarpa: f	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinium vitis-idaea	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sparganium eurycarpum	0.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex tenera	0.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eriophorum brachyantherum	0.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Utricularia vulgaris	17	490	37	.	.	.	.	.	.	.	.	.	.	.	0.3
Myriophyllum exalbescens	0.4	31	12	.	.	.	.	.	.	.	.	.	.	.	.
Lemna minor	0.3	22	19	.	.	.	.	.	.	.	.	.	.	.	.
Sparganium minimum	2.0	11	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus gmelinii	10	.	0.4	.	.	.	.	.	.	.	.	.	8.7	.	.
Lemna trisulca	.	17	38	.	.	.	.	.	.	.	.	.	.	.	.
Ceratophyllum demersum	.	3.5	5.0	.	.	.	.	.	.	.	.	.	.	.	.
Alisma plantago-aquatica	.	1.0	0.3	.	.	.	.	.	.	.	.	.	.	.	.
Nuphar variegatum	.	102	.	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton richardsonii	.	74	.	.	.	.	.	.	.	.	.	.	.	.	.

Appendix 9. (Cont'd)

	16	2	4	6	5	7	8	9	10	11	12	13	15	14	3
	16[c]	10	9	8	13	22	7	19	3	12	8	14	3	5	6
P. zosteriformis	.	62	.	.	.	.	.	.	.	.	.	.	.	.	.
P. gramineus	.	2.4	.	.	.	.	.	.	.	.	.	.	.	.	.
P. pusillus	.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus macounii	.	.	38	11	16	19	.	1.0	.	.	.	.	.	4.4	.
Carex sychnocephala	.	.	28	.	.	6.8	4.9	3.5	.	.	.	.	.	.	0.3
Beckmannia syzigachne	.	.	2.8	2.6	4.8	17	4.4	.	.	.	.	.	.	.	.
Deschampsia caespitosa	.	.	0.4	.	0.2	40	22	.	.	.	.	.	.	.	.
Scolochloa festucacea	.	.	92	0.2	0.2	0.1	.	.	.	.	.	.	.	.	.
Polygonum amphibium	.	.	14	12	31	17	.	.	.	.	.	.	.	4.2	.
Salix petiolaris	.	.	15	1.0	9.5	3.3	.	.	.	.	.	.	.	.	.
Ranunculus pensylvanicus	.	.	16	0.6	3.8	1.4	.	.	.	.	.	.	.	.	.
Stachys palustris	.	.	3.2	1.8	3.2	3.1	.	.	.	.	.	.	.	.	.
Alopecurus aequalis	.	.	0.4	.	.	0.2	.	.	.	.	.	.	.	.	0.3
Glyceria grandis	.	.	43	0.5	16	.	.	.	.	.	.	.	.	.	.
Ranunculus natans	.	.	15	0.2	0.3	.	.	.	.	.	.	.	.	.	.
R. sceleratus	.	.	7.8	0.2	.	.	.	0.3	.	.	.	.	.	.	.
Urtica gracilis	.	.	.	1.2	0.2	.	.	.	.	.	.	.	.	.	.
Acorus calamus: f	.	.	3.0	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus aquatilis	.	.	2.8	.	.	.	.	.	.	.	.	.	.	.	.
R. pedatifidus	.	.	0.9	.	.	.	.	.	.	.	.	.	.	.	.
Sonchus arvensis	.	.	0.9	.	.	.	.	.	.	.	.	.	.	.	.
Geum allepicum	.	.	.	16	0.2	0.1	.	.	.	.	.	.	.	0.4	.
Polygonum lapathifolium	.	.	.	9.1	6.5	.	.	.	.	.	.	.	.	.	.
Salix bebbiana	.	.	.	7.8	6.0	15	0.4	40	37	18	0.2	1.5	46	0.8	.
Populus balsamifera	.	.	.	3.2	.	2.4	0.7	3.3	6.3	1.4	8.5	0.4	.	.	.
Salix lutea	.	.	.	.	19	4.6	4.7	44	10	26	.	.	.	.	.
Plantago major	.	.	.	.	.	15	0.3	7.8	7.3	3.1	.	.	.	.	0.5
Eleocharis palustris	.	.	.	.	24	17	15	1.4	.	.	.	.	.	.	17
Puccinellia nuttalliana	.	.	.	.	1.8	6.7	.	1.1	.	.	.	.	.	.	.
Phalaris arundinacea	.	.	.	.	0.7	20	23	.	.	.	.	.	.	.	.
Phragmites communis	.	.	.	.	.	74	4.9	.	.	.	.	.	.	.	.
Erigeron lonchophyllus	.	.	.	.	0.6	15	.	.	.	.	.	.	.	.	.
Hippuris vulgaris	.	.	.	.	2.3	2.4	.	.	.	.	.	.	.	.	.
Equisetum arvense	.	.	.	.	.	4.6	3.1	165	1.7	14	.	.	.	.	.
Salix interior	.	.	.	.	.	27	16	57	35	14	.	.	.	.	.
Equisetum palustre	.	.	.	.	.	3.4	4.9	24	31	19	.	.	.	.	.
Melilotus alba: f	.	.	.	.	.	0.3	.	8.2	.	0.2	.	.	.	.	.
Agropyron trachycaulum	0.2	.	.	.	.	.	.	4.5	0.7	3.1	.	.	.	.	.
Limosella aquatica	.	.	.	.	.	2.5	3.6	0.5	.	.	.	.	.	.	0.3
Carex bebbii	.	.	.	.	.	1.2	.	0.2	.	0.2	.	.	.	.	1.0
Ranunculus cymbalaria	.	.	.	.	.	0.2	0.3	.	1.0	.	.	.	.	.	0.3
Eleocharis acicularis	.	.	.	.	.	7.3	4.6	0.2	.	.	.	.	.	.	3.2
Juncus alpinus	.	.	.	.	.	5.8	11	14	.	.	.	.	.	.	.
Hordeum jubatum	.	.	.	.	.	17	0.4	1.0	.	.	.	.	.	.	.
Juncus nodosus	.	.	.	.	.	6.0	1.1	1.3	.	.	.	.	.	.	.
Potentilla anserina	.	.	.	.	.	0.6	.	8.2	.	.	.	.	.	.	0.3
Senecio congestus	.	.	.	.	.	0.2	1.1	.	.	.	.	.	.	.	0.7
Solidago graminifolia	.	.	.	.	.	0.5	0.3	.	.	.	.	.	.	.	.
Aster pansus	.	.	.	.	.	15	.	.	.	.	.	.	.	.	.
Artemisia campestris: f,g,h	.	.	.	.	.	11	.	.	.	.	.	.	.	.	.
Taraxacum officinale	.	.	.	.	.	3.1	.	.	.	.	.	.	.	.	.
Polygonum aviculare	.	.	.	.	.	1.4	.	.	.	.	.	.	.	.	.
Phleum pratense	.	.	.	.	.	0.6	.	.	.	.	.	.	.	.	.
Chenopodium album	.	.	.	.	.	0.4	.	.	.	.	.	.	.	.	.
Dracocephalum nuttallii	.	.	.	.	.	0.3	.	.	.	.	.	.	.	.	.
Equisetum laevigatum: f	.	.	.	.	.	0.1	.	.	.	.	.	.	.	.	.
Ranunculus flammula: f	.	.	.	.	.	0.1	.	.	.	.	.	.	.	.	.
Mimulus guttatus: f,g,h	.	.	.	.	.	.	.	0.2	.	.	.	.	.	.	.
Chenopodium leptophyllum	.	.	.	.	.	.	.	0.1	.	.	.	.	.	.	.
C. capitatum	.	.	.	.	.	.	.	0.1	.	.	.	.	.	.	.
Collomia linearis	.	.	.	.	.	.	.	0.1	.	.	.	.	.	.	.
Kochia scoparia: f,h	.	.	.	.	.	.	.	0.1	.	.	.	.	.	.	.
Cornus stolonifera	.	.	.	.	.	.	.	1.2	.	34	43	8.5	60	0.4	.
Pyrola asarifolia	1.4	.	.	.	.	.	.	.	.	.	7.9	56	28	1.2	.
Rubus strigosus	.	.	.	.	.	.	.	.	.	2.1	0.2	13	0.7	.	.
Poa pratensis	.	.	.	.	.	.	.	.	.	0.2	0.5	.	6.3	4.6	.
Aster ciliolatus	.	.	.	.	.	.	.	.	0.7	0.5	.	0.4	0.7	0.4	.
Solidago lepida	.	.	.	.	.	.	.	.	.	0.2	.	0.7	.	0.4	.
Cinna latifolia	.	.	.	.	.	.	.	.	.	0.2	1.1	0.4	.	.	.
Rubus pubescens	.	.	.	.	.	.	.	.	.	7.2	.	26	.	.	.
Rosa acicularis	.	.	.	.	.	.	.	.	.	.	69	83	22	.	.
Viburnum edule	.	.	.	.	.	.	.	.	.	.	0.4	114	21	.	.
Mertensia paniculata	.	.	.	.	.	.	.	.	.	.	16	25	42	.	.
Pyrola secunda	0.2	.	.	.	.	.	.	.	.	.	0.4	22	16	.	.
Shepherdia canadensis	.	.	.	.	.	.	.	.	.	.	1.6	15	1.7	.	.
Aralia nudicaulis	.	.	.	.	.	.	.	.	.	.	16	6.5	.	.	.
Galium triflorum	.	.	.	.	.	.	.	.	.	.	7.9	4.9	.	.	.
Ribes triste	.	.	.	.	.	.	.	.	.	.	0.2	0.3	.	.	.
Lathyrus ochroleucus	.	.	.	.	.	.	.	0.2	.	.	.	7.5	0.7	0.6	.
Betula papyrifera	.	.	.	.	.	1.0	.	.	.	.	.	0.1	4.3	3.3	.
Linnaea borealis	1.4	.	.	.	.	.	.	.	.	.	.	41	38	.	.
Geocaulon lividum	.	.	.	.	.	.	.	.	.	.	.	0.5	72	.	.
Ribes oxyacanthoides	.	.	.	.	.	.	.	.	.	1.1	.	40	27	.	.
Arctostaphylos uva-ursi	1.2	.	.	.	.	.	.	.	.	.	.	13	53	.	.
Cornus canadensis	.	.	.	.	.	.	.	.	.	.	.	56	7.7	.	.
Rubus acaulis	.	.	.	.	.	.	.	.	.	.	.	7.7	22	.	.
Mitella nuda	.	.	.	.	.	.	.	.	.	.	.	11	8.7	.	.
Ribes hudsonianum	.	.	.	0.8	.	.	.	.	.	.	.	0.3	1.7	.	.
Viola adunca	.	.	.	.	.	.	.	.	.	.	.	0.2	1.0	.	.
Elymus innovatus	.	.	.	.	.	.	.	.	.	.	.	0.1	0.7	.	.
Galium boreale	.	.	.	.	.	.	.	.	.	.	.	15	.	.	.
Maianthemum canadense	0.2	.	.	.	.	.	.	.	.	.	.	12	.	.	.
Actaea rubra	.	.	.	0.2	.	.	.	.	.	.	.	3.8	.	.	.
Viola nephrophila	.	.	.	.	.	.	.	.	.	.	.	2.3	.	.	.
Amelanchier alnifolia	.	.	.	.	.	.	.	.	.	.	.	0.6	.	.	.
Pyrola virens	.	.	.	.	.	.	.	.	.	.	.	0.5	.	.	.
Poa interior: h	.	.	.	.	.	.	.	.	.	.	.	0.2	.	.	.
Campanula rotundifolia	.	.	.	.	.	.	.	.	.	.	.	0.2	.	.	.
Symphoricarpos albus	.	.	.	.	.	.	.	.	.	.	.	0.2	.	.	.

Appendix 9. (Cont'd)	16	2	4	6	5	7	8	9	10	11	12	13	15	14	3
	16[c]	*10*	*9*	*8*	*13*	*22*	*7*	*19*	*3*	*12*	*8*	*14*	*3*	*5*	*6*
Saxifraga tricuspidata: g	.	.	.	.	.	.	.	.	.	.	.	0.1	.	.	.
Polypodium vulgare	.	.	.	.	.	.	.	.	.	.	.	0.1	.	.	.
Thalictrum venulosum	.	.	.	.	.	.	.	.	.	.	.	0.1	.	.	.
Carex concinna	.	.	.	.	.	.	.	.	.	.	.	.	1.0	.	.
Petasites palmatus	.	.	.	.	.	.	.	.	.	.	.	.	1.0	.	.
P. frigidus: f	.	.	.	.	.	.	.	.	.	.	.	.	0.7	.	.
Scirpus microcarpus: f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.3
Utricularia intermedia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.3
Calamagrostis canadensis	25	.	28	125	100	36	0.4	.	1.0	0.2	0.2	17	34	11	3.2
Picea glauca	0.3	.	.	0.5	10	2.1	.	3.5	86	12	0.6	7.6	35	26	.
Mentha arvensis	1.4	.	0.7	22	28	38	0.9	0.2	7.3	1.8	.	0.2	.	1.0	.
Alnus tenuifolia	8.1	.	.	.	1.5	6.4	.	0.1	93	26	16	1.8	12	1.6	.
Poa palustris	.	.	0.2	13	16	17	.	0.2	.	0.5	0.4	8.1	7.7	1.8	.
Potentilla norvegica	.	.	.	6.4	2.3	4.1	.	1.1	8.7	0.5	.	0.6	2.0	1.0	0.7
Equisetum fluviatile	14	.	.	.	12	2.0	0.4	0.2	101	2.5	.	.	7.7	.	130
Rorippa islandica	.	.	66	1.0	2.5	4.5	0.3	16	6.3	0.4	.	.	.	.	10
Carex atherodes	.	7.8	373	387	329	121	22	.	.	.	.	.	.	35	45
Equisetum pratense	.	.	.	1.0	.	0.2	.	.	10	20	120	82	3.0	52	.
Scutellaria galericulata	.	.	18	61	22	4.3	.	.	30	.	0.4	5.0	.	0.6	.
Sium suave	9.4	.	2.9	2.8	34	15	.	.	.	.	.	0.2	1.0	0.6	.
Erigeron philadelphicus	.	.	9.2	12	0.5	1.9	.	0.2	.	0.9	.	0.3	.	0.8	.
Stellaria longifolia	0.6	.	.	14	0.2	0.6	0.3	.	.	.	.	2.1	.	0.4	0.3
Epilobium angustifolium	.	.	.	.	.	3.3	.	8.2	185	.	0.2	15	.	0.4	0.3
Typha latifolia	6.2	.	7.0	.	9.7	13	80	.	1.0	.	.	.	.	.	84
Fragaria vesca	7.4	.	.	2.0	.	.	.	0.2	.	2.2	48	15	67	.	.
Galium trifidum	8.6	.	18	26	17	11	.	.	.	.	.	.	6.3	1.2	.
Epilobium glandulosum	.	.	10	22	7.8	6.7	.	5.1	1.0	7.7	.	.	.	.	.
Juncus balticus	.	.	0.2	.	0.4	1.5	0.3	1.3	.	1.9	.	.	.	.	0.3
Carex aquatilis	78	.	0.4	.	.	26	8.4	0.4	.	.	.	.	26	.	.
Salix pyrifolia	11	.	5.3	.	15	20	.	16	.	.	.	.	7.7	.	.
Carex retrorsa	29	.	.	.	.	3.0	19	7.4	.	1.6	.	.	1.0	.	.
Agrostis scabra	.	.	.	.	.	8.3	.	.	.	0.2	1.2	1.3	1.3	2.0	.
Sparganium angustifolium	.	1.9	2.9	.	.	0.9	0.7	1.2	.	.	.	.	.	.	4.7
Arenaria lateriflora	.	.	.	0.5	.	.	.	.	.	.	0.2	0.3	0.7	4.2	0.7
Scirpus validus	.	.	0.3	.	0.3	11	8.7	.	.	.	.	.	.	.	42
Rumex maritimus	.	.	40	.	.	0.4	0.9	0.7	.	.	.	.	.	.	0.3
Artemisia biennis	.	.	.	.	.	10	.	30	.	0.8	.	0.1	.	.	0.3
Stellaria crassifolia	14	.	5.3	5.6	11	0.3	.	.	.	.	.	.	.	.	.
Juncus bufonius	.	.	3.7	.	0.2	1.9	0.3	0.2	.	.	.	.	.	.	.
Achillea millefolium	.	.	.	.	.	0.1	.	.	0.7	0.2	.	1.9	1.0	.	.
Glyceria striata	.	33	.	.	0.2	0.2	.	.	.	.	.	.	.	.	30
Sphenopholis obtusata: f	.	.	.	.	.	.	.	0.2	6.3	.	0.2	.	.	3.6	.
Geum macrophyllum	.	.	.	1.6	0.2	.	.	.	.	.	.	4.7	.	0.8	.
Carex rostrata	5.6	.	0.7	.	0.6	0.1	.	.	.	.	.	.	.	.	.
Petasites vitifolius	3.9	.	.	0.4	.	.	.	.	.	.	.	0.1	1.0	.	.
Cicuta douglasii	2.5	.	0.2	0.2	.	.	.	.	.	.	.	0.1	.	.	.
Bidens cernua	3.1	.	52	.	.	.	.	0.1	.	.	.	.	.	.	.
Lysimachia thyrsiflora	25	.	.	.	.	.	.	.	1.0	.	.	.	.	.	0.5
Vicia americana	.	.	.	.	.	9.1	.	0.2	.	.	.	2.0	.	.	.
Populus tremuloides	.	.	.	.	.	1.3	.	.	.	.	.	0.1	.	0.6	.
Aster puniceus	.	.	.	0.8	.	.	.	.	.	0.2	.	.	.	0.4	.
Achillea sibirica	.	.	.	.	.	.	.	0.1	.	0.2	.	0.6	.	.	.
Potentilla palustris	74	.	.	.	.	0.3	.	.	.	.	.	.	.	.	.
Anemone canadensis	.	.	.	2.9	.	.	.	.	.	.	.	9.1	.	.	.
Sagittaria cuneata	.	4.2	.	.	.	.	.	.	.	.	.	.	.	.	0.5
Fragaria virginiana	.	.	.	.	.	.	.	0.2	.	.	.	2.2	.	.	.
Salix pseudomonticola	.	.	.	.	.	0.6	.	.	.	.	.	1.6	.	.	.
Triglochin maritima	0.9	.	.	.	.	.	1.0	.	.	.	.	.	.	.	.
Parnassia palustris	.	.	.	.	.	.	.	.	.	.	.	.	1.0	.	0.3
Salix lasiandra	.	.	.	.	.	0.9	.	.	.	0.2	.	.	.	.	.
Rumex mexicanus	.	.	.	0.2	.	.	.	.	.	.	.	0.1	.	.	.
Heracleum lanatum	.	.	.	0.2	.	.	.	.	.	.	.	0.1	.	.	.
Equisetum hyemale	.	.	.	.	0.2	.	.	0.3	.	.	.	.	.	.	.
Sisyrinchium montanum	.	.	.	.	.	.	.	.	.	0.2	.	.	.	.	.
Calamagrostis inexpansa	26[e]	.	.	.	.	.	.	.	.	.	.	.	30[e]	.	.
Betula glandulosa	20	.	.	.	.	.	.	.	.	.	.	.	21	.	.
Smilacina trifolia	36	.	.	.	.	.	.	.	.	.	.	.	1.0	.	.
Epilobium palustre	11	.	.	.	.	.	.	.	.	.	.	.	26	.	.
Salix barklayi (?): f,g	3.9	.	.	.	.	.	.	.	.	.	.	.	30	.	.
Equisetum scirpoides	0.1	.	.	.	.	.	.	.	.	.	.	.	25	.	.
Oxycoccus microcarpus	14	.	.	.	.	.	.	.	.	.	.	.	0.7	.	.
Carex canescens	4.1	.	.	.	.	.	.	.	.	.	.	.	1.0	.	.
Salix myrtillifolia	2.8	.	.	.	.	.	.	.	.	.	.	.	1.0	.	.
Equisetum sylvaticum	0.1	.	.	.	.	.	.	.	.	.	.	.	2.0	.	.
Addendum i,j															
Carex arcta	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
C. gynocrates	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
C. loliacea	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster hesperius	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Lactuca pulchella	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Astragalus occidentalis: f	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Moneses uniflora	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Eriophorum viridi-carinatum: f	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.

a 2. Vascular Aquatic, 3. Herb Immature Marsh, 4. Wet Meadow, 5. Meadow, 6. Fen, 7. Marsh, 8. Shrub Immature Marsh, 9. Levee Herb, 10. Swale Shrub, 11. Levee Shrub, 12. Levee Tree, 13. Upland Forest, 14. Moist Lowland Forest, 15. Wet Lowland Forest, 16. Bog.
b 1. Algal Aquatic. This community type has no vascular species but non-rooted stem fragments of *Potamogeton pectinatus* were found in waters of the Lake Athabasca Marsh study area.
c Number of communities per community type.
d Mean prominence value.
e Considered a species group because Bog and Wet Lowland Forest Community Types occur beside each other in the Nuphar Lake study area.
f New species record for the Peace Athabasca delta based on species lists of Raup (1935) and Gentle (1973).
g Species associated with the Cordilleran Region.
h Species associated with the Prairie Region.
i Species present in the study region but not recorded in the quantitative analysis. Presence is indicated by a '+'.
j See Tables 30,31 for other species present in the study region.
A Mean number of species in stratum of community type.